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Guide to Contributors

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Comparaison du climat marin de Grande-Rivière (baie des Chaleurs) avec celui d'autres stations de la côte atlantique[1,2]

PAR L. M. LAUZIER[3] ET A. MARCOTTE[4]

RÉSUMÉ

Les variations de la température des eaux de surface à Grande-Rivière entre 1938 et 1962 ont été étudiées pour établir une norme du climat marin de la région et signaler les cas qui s'en écartent. Avec une moyenne annuelle de 5.0 C, la température de surface à Grande-Rivière oscille entre −1.5 et 14.0 C de février à août, respectivement. Les eaux ont une température inférieure à 4.0 C pendant 180 jours, soit environ la moitié de l'année. Les moyennes mensuelles sont toujours plus élevées à l'île d'Entrée qu'à Grande-Rivière, et plus élevées à Borden qu'à l'île d'Entrée. En été cette différence de température atteint 3.0 C entre l'île d'Entrée et Grande-Rivière et 5.0 C entre Borden et Grande-Rivière. Les années froides ou chaudes à Borden et à l'île d'Entrée ne correspondent pas nécessairement à celles de Grande-Rivière, où les années typiquement chaudes ou froides sont peu nombreuses.

La quantité de chaleur absorbée à la surface, l'échange de chaleur entre les différentes nappes d'eau et l'apport de chaleur par les courants diffèrent suivant les régions du golfe Saint-Laurent. Ces facteurs semblent expliquer les variations locales du climat marin. Les variations à long terme de la température des eaux de surface enregistrées en quelques points de la côte de l'est du Canada ont servi de points de comparaison. À Grande-Rivière, ces variations sont semblables à celles des eaux du large de la Nouvelle-Écosse, tandis que celles des régions peu profondes du plateau des Îles-de-la-Madeleine semblent être différentes des autres, alors que le réchauffement se continue sur une période plus longue qu'à Grande-Rivière.

ABSTRACT

Temperature variations of surface waters at Grande-Rivière have been studied in order to describe the marine climate of the region and to show anomalies between 1938 and 1962. Monthly averages of surface temperatures at Grande-Rivière vary between −1.5 and 14.0 C from February to August, respectively, yielding an annual mean of 5.0 C. Temperatures of surface waters are lower than 4.0 C during approximately 6 months of the year. Monthly averages are always higher at Entry Island than at Grande-Rivière and higher at Borden than at Entry Island. Summertime difference in temperature reaches 3.0 C between Entry Island and Grande-Rivière and 5.0 C between Borden and Grande-Rivière. Warm or cold years at Borden and at Entry Island are not necessarily warm or cold at Grande-Rivière.

Heat exchanges at the surface and between layers and advection of heat are taken into consideration to explain the local variations of the marine climate at various parts of the Gulf of St. Lawrence. Long-term variations of surface water temperature at Grande-Rivière are compared with those observed at other points along Canada's east coast. Such variations at Grande-Rivière are similar to those of the waters off Nova Scotia. However, they seem to be different from those of other areas of the Magdalen Shallows where warming continues over a longer period than at Grande-Rivière.

[1]Received for publication June 15, 1965.
[2]Travaux sur les Pêcheries du Québec, no 10. Division des Pêcheries, Ministère de l'Industrie et du Commerce, Québec, Canada.
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J. FISH. RES. BD. CANADA, **22**(6), 1965.
Printed in Canada.

INTRODUCTION

Depuis 1938, les chercheurs de la Station biologique de Grande-Rivière poursuivent des observations sur la température des eaux de surface à Grande-Rivière dans le but d'en étudier les variations saisonnières, de même que les variations annuelles et leur influence sur la progression des phénomènes biologiques particuliers à la région. Jusqu'en 1954, les observations se faisaient habituellement à partir du mois de mai et se continuaient jusqu'au mois de septembre, parfois jusqu'en novembre ou décembre.

La longue série d'observations des températures estivales fut inaugurée en 1938, alors que la Station biologique du Saint-Laurent de l'Université Laval s'établissait à Grande-Rivière. Cette série a été continuée par la Station de Biologie marine, et, depuis 1955, les lectures de température se font quotidiennement durant toute l'année. Les données ainsi recueillies ont déjà été présentées sous forme de graphiques dans les rapports annuels de chaque institution (Tremblay, 1943–50; Marcotte, 1952–53, 1959–63).

Pour notre part, nous avons fait l'analyse des lectures de température ainsi enregistrées à Grande-Rivière de 1938 à 1962. Nous en présentons ici les résultats en montrant les variations saisonnières, l'évolution moyenne de la température, les écarts d'une année à l'autre, les valeurs mensuelles extrêmes, de même que les variations à long terme. Nous voulons aussi montrer les différences qui existent entre les variations de températures observées à Grande-Rivière et celles se présentant à d'autres stations de la côte est du Canada, soit l'île d'Entrée, Borden, Bateau-phare Sambro, et St. Andrews (Fig. 1). Finalement nous voulons mettre en lumière quelques-uns des facteurs qui entrent en jeu dans les différents régimes de température.

MÉTHODES D'OBSERVATION ET DE COMPILATION

Les observations quotidiennes de température de l'eau de surface, au dixième de degré centigrade, se font le matin à 8 heures, au quai de Grande-Rivière (48°23′33″N, 64°29′40″W). La température de l'air, le vent et les données météorologiques générales sont alors notées.

Au lieu de présenter ici l'évolution quotidienne des températures pour chacune des 25 années, de 1938 à 1962, nous avons cru préférable de calculer les moyennes par période de 10 jours et de faire les moyennes mensuelles pour chaque année (Tableau I). Les moyennes mensuelles ont été calculées à partir des moyennes trimensuelles. Nous avons choisi cette méthode parce que jusqu'en 1954 les observations commençaient au printemps pour se terminer à l'automne. En calculant ainsi les moyennes par périodes de 10 jours, on pouvait utiliser un plus grand nombre d'observations que dans le cas des moyennes de 30 jours. Dans certains cas des moyennes de 10 jours ont été interpolées ou extrapolées: les moyennes mensuelles apparaissent alors entre parenthèses dans le Tableau I. Les moyennes des Tableaux I et II ne sont pas nécessairement les mêmes que celles de Marcotte (1964). Ces dernières ont été calculées à partir des données disponibles pendant un mois donné, représentant parfois une moyenne soit de la première ou de la dernière moitié du mois.

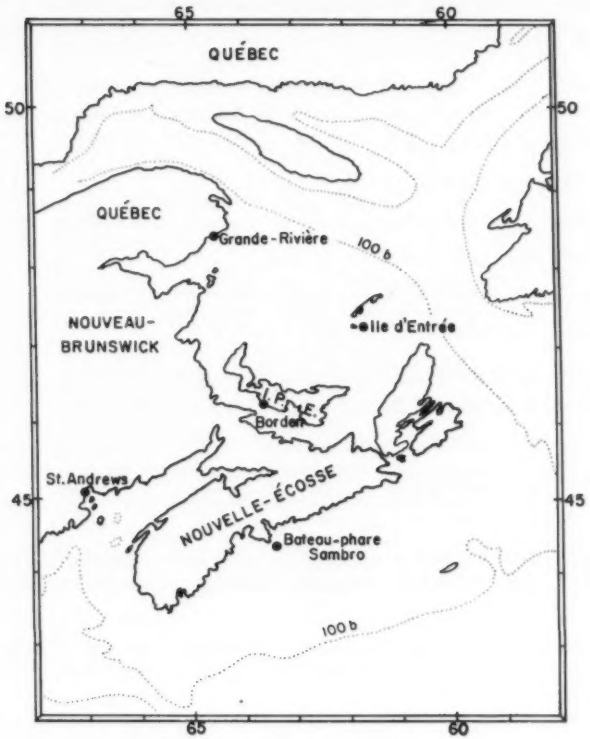

FIG. 1. Carte de la région.

ANALYSE DES DONNÉES

VARIATIONS SAISONNIÈRES

La grande moyenne de chacune des périodes de 10 jours, portée sur un graphique en fonction du temps (Fig. 2), fait voir la variation moyenne de la température de surface au quai de Grande-Rivière. On peut déduire de ce graphique que les eaux de surface ont une température moyenne plus basse que 0.0 C du 23 décembre au 10 avril; les eaux ont une température inférieure à 4.0 C pendant 180 jours, soit environ la moitié de l'année. Par contre, en général, elles ont une température supérieure à 12.0 C pendant 66 jours. Le minimum moyen, −1.5 C, est atteint au milieu de février, et le maximum moyen, 14.2 C, au commencement d'août. Le réchauffement des eaux a son point culminant en juin alors qu'il atteint une valeur moyenne de 0.17 C par jour. Par contre, à l'automne, le refroidissement est sensiblement plus lent que le réchauffement au printemps; la température monte de 4.0 à 12.0 C en 53 jours au printemps, elle baisse de 12.0 à 4.0 C en 65 jours à l'automne.

TABLEAU I. Moyennes mensuelles de la température de surface à Grande-Rivière, 1938–62.

Année	Jan.	Fév.	Mars	Avril	Mai	Juin	Juil.	Août	Sept.	Oct.	Nov.	Déc.
1938	—	—	—	—	3.7	10.6	(13.7)	14.1	—	—	—	—
1939	—	—	—	—	3.7	10.1	—	—	—	—	—	—
1940	—	—	—	—	(3.3)	7.7	12.5	14.8	11.4	8.2	—	—
1941	—	—	—	—	3.6	7.6	11.5	12.7	(9.9)	—	—	—
1942	—	—	—	—	(5.9)	9.5	13.2	13.7	(10.3)	—	—	—
1943	—	—	—	—	2.9	7.3	13.1	13.3	(12.0)	—	—	—
1944	—	—	—	—	3.6	8.5	14.0	14.5	13.2	7.4	4.2	—
1945	—	—	—	—	3.8	8.8	13.8	14.1	11.8	(7.3)	—	—
1946	—	—	—	—	3.4	8.4	10.8	14.0	—	—	—	—
1947	—	—	—	—	(2.2)	7.7	14.0	14.3	10.8	—	—	—
1948	—	—	—	—	(3.8)	8.1	13.9	14.8	12.6	—	—	—
1949	—	—	—	—	4.8	9.0	14.0	14.4	10.4	—	—	—
1950	—	—	—	—	—	8.6	10.7	13.6	(11.5)	—	—	—
1951	—	—	—	—	(4.6)	9.7	13.2	15.2	12.6	7.2	3.2	—
1952	—	—	—	—	(4.2)	9.9	14.9	16.1	12.3	6.8	—	—
1953	—	—	—	—	5.0	8.9	13.1	13.3	10.6	7.2	4.6	—
1954	—	—	—	(0.3)	4.4	9.5	12.6	12.0	11.3	7.3	3.8	1.2
1955	-0.9	-1.3	-1.3	1.3	5.3	9.8	15.6	15.1	11.0	7.3	4.4	1.0
1956	-0.8	-1.3	-1.2	0.2	3.2	7.9	12.1	12.9	10.7	6.7	4.0	0.4
1957	-1.4	-1.1	-1.1	0.1	3.8	8.7	10.7	14.2	11.0	7.1	4.4	0.9
1958	-1.0	-1.5	-0.7	1.1	4.7	7.9	12.6	13.5	10.6	7.1	3.8	-0.3
1959	-1.3	-1.6	-1.4	1.0	4.3	7.9	13.5	14.4	12.7	8.0	3.6	0.4
1960	-1.4	-1.4	-1.4	-0.2	4.6	10.3	13.0	12.6	10.5	6.7	3.2	(0.4)
1961	-1.6	-1.7	-1.3	0.3	3.8	8.1	12.7	13.7	11.2	8.4	4.9	2.3
1962	-0.7	-1.8	-0.9	0.6	3.9	9.1	10.7	13.2	11.3	8.5	4.5	1.4
Moyenne 1938–62	-1.1	-1.5	-1.2	0.5	4.1	8.8	12.9	13.9	11.4	7.5	4.0	0.8

TABLEAU II. Température mensuelles normales, maxima et minima, à Grande-Rivière.

Mois	Période	Nombre d'années	Moyenne	Maximum	Minimum
Janvier	1955–62	8	−1.1	−0.7 (1962)	−1.6 (1961)
Février	"	8	−1.5	−1.1 (1957)	−1.8 (1962)
Mars	"	8	−1.2	−0.7 (1958)	−1.4 (1959)
Avril	1954–62	9	0.5	1.3 (1955)	−0.2 (1960)
Mai	1938–62	24	4.1	5.9 (1942)	2.2 (1947)
Juin	"	25	8.8	10.6 (1938)	7.3 (1943)
Juillet	"	24	12.9	15.6 (1955)	10.7 (1950, 1957, 1962)
Août	"	24	13.9	16.1 (1952)	12.0 (1954)
Septembre	1940–62	22	11.4	13.2 (1944)	9.9 (1941)
Octobre	"	15	7.5	8.5 (1962)	6.7 (1956, 1960)
Novembre	1944–62	12	4.0	4.9 (1961)	3.2 (1951, 1960)
Décembre	1954–62	9	0.8	2.3 (1961)	−0.3 (1958)

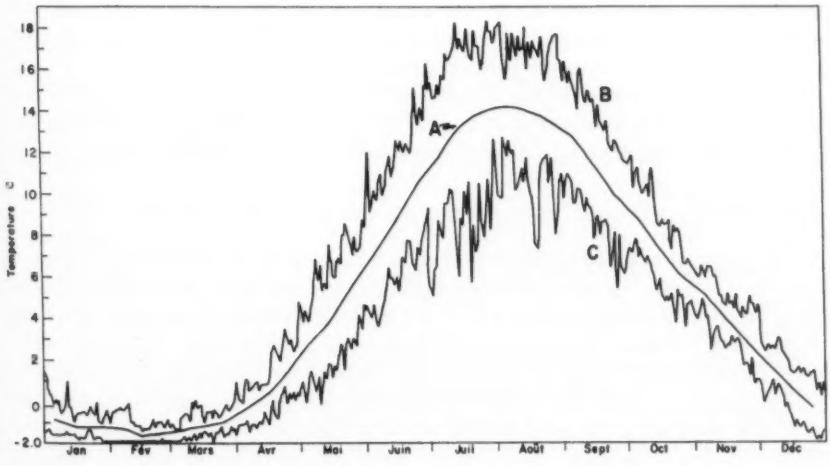

FIG. 2. Variation moyenne (A) de la température des eaux superficielles à Grande-Rivière, par périodes de 10 jours. Ecart quotidien à Grande-Rivière, maximum (B) et minimum (C) observés pendant la période 1938–62.

Écarts de température et variations d'une année à l'autre à Grande-Rivière

L'écart des températures de surface, pour une date ou une période donnée de l'année est très grand. Les températures varient plus largement en été qu'en hiver. La Fig. 2 fait aussi voir les écarts quotidiens, soit le maximum et le minimum observés à une date déterminée, pendant la période 1938–62.

Durant les mois d'été, l'écart moyen est de 4.0 à 5.0 C, mais il est parfois de l'ordre de 9.0 C. En hiver, il est normalement de l'ordre de 1.0 C. L'écart de température très prononcé en été, par rapport aux autres mois de l'année, est simplement dû à la nature même de la colonne d'eau, très stratifiée au printemps et en été mais plutôt uniforme aux autres moments de l'année. Les mouvements de montée le long des côtes, dus à l'action du vent, apportent vers la surface des eaux froides, provenant des couches profondes (Tremblay et Lauzier, 1942).

Le Tableau II donne un aperçu des écarts moyens de température pour chacun des mois de l'année; il rapporte les températures maximum et minimum et la grande moyenne mensuelle pour les eaux de surface à Grande-Rivière. Après avoir étudié les écarts quotidiens, il ne faut pas s'étonner de constater que les écarts mensuels atteignent un maximum en été, soit 4.9 et 4.1 C en juillet et août, respectivement. Les variations d'une année à l'autre, ou les déviations à partir de la normale, sont telles que les années typiquement chaudes ou typiquement froides sont peu nombreuses. Par contre, on observe souvent une saison chaude ou froide, mais elle peut être suivie la même année par une saison froide ou chaude suivant le cas. Ainsi pour les eaux de surface à Grande-Rivière, en 1943 et 1947, un printemps (mai et juin) très froid a laissé place à un été (juillet et août) moyen ou chaud. En 1950 et 1954, un été froid avait suivi un printemps plutôt chaud. En 1961, un été normal et un automne chaud ont succédé à un hiver très froid et à un printemps tardif.

Durant la période 1938–62, les années 1941 et 1956 sont considérées comme étant typiquement froides et les années 1952 et 1955, typiquement chaudes. Poirier (1958) considérait déjà ces deux dernières années comme telles.

Comparaison avec d'autres points du golfe Saint-Laurent

Le Tableau III donne les moyennes mensuelles de température des eaux de surface et leurs valeurs extrêmes pour chacun des mois de l'année à deux points du golfe Saint-Laurent: à l'île d'Entrée, Îles-de-la-Madeleine, de 1930 à 1962, et à Borden, Île-du-Prince-Édouard, de 1951 à 1962, (Lauzier, MS, 1953; Lauzier et Hull, 1961; et dossiers de la Station biologique de St. Andrews).

En comparant les données des Tableaux II et III, on voit que les moyennes mensuelles sont toujours plus élevées à l'île d'Entrée qu'à Grande-Rivière et plus élevées à Borden qu'à l'île d'Entrée. En été, cette inégalité de température atteint 3.0 C entre l'île d'Entrée et Grande-Rivière, et 5.0 C entre Borden et Grande-Rivière. De plus, durant la période de juillet à octobre, les températures moyennes à Grande-Rivière sont plus basses que les températures minimales à

TABLEAU III. Température mensuelles normales, maxima et minima, à l'île d'Entrée, Îles-de-la-Madeleine, et à Borden, Île-du-Prince-Édouard.

Mois	Nombre d'années	Moyenne	Maximum	Minimum
a) *Île d'Entrée*				
Avril	21	1.0	3.8 (1951)	−0.4)1948)
Mai	33	4.9	7.4 (1960)	2.4 (1961)
Juin	32	9.8	12.2 (1960)	7.5 (1961)
Juillet	33	14.9	17.3 (1960)	13.3 (1962)
Août	33	17.2	18.7 (1945)	15.1 (1954)
Septembre	31	14.8	16.8 (1934)	12.2 (1941)
Octobre	33	10.0	11.9 (1946)	8.3 (1940, 1941)
Novembre	30	5.2	7.0 (1961)	2.5 (1933)
Décembre	24	0.8	2.6 (1944, 1950)	−0.8 (1940)
b) *Borden*				
Janvier	11	−1.1	−0.6 (1955)	−1.8 (1953)
Février	11	−1.2	−0.3 (1960)	−1.8 (1954)
Mars	11	−0.8	0.4 (1958)	−1.3 (1956)
Avril	11	1.2	2.8 (1953)	−0.2 (1961)
Mai	11	6.8	8.5 (1960)	1.3 (1961)
Juin	12	12.8	14.1 (1960)	9.2 (1961)
Juillet	12	17.5	18.6 (1959)	15.7 (1962)
Août	12	19.0	20.1 (1960)	17.6 (1961)
Septembre	12	17.0	17.6 (1951, 52, 60)	15.9 (1956)
Octobre	12	11.9	13.7 (1961)	10.9 (1958)
Novembre	12	6.4	7.9 (1961)	5.0 (1952)
Décembre	12	1.0	2.9 (1953)	−1.0 (1955)

l'île d'Entrée. Il en est de même pour les températures moyennes à l'île d'Entrée par comparaison avec les températures minimales à Borden.

La variation moyenne de la température est très différente à Grande-Rivière, à l'île d'Entrée et à Borden, non seulement dans le niveau moyen mais aussi dans le taux de réchauffement au printemps et de refroidissement à l'automne. À l'encontre des conditions observées à Grande-Rivière, le taux de réchauffement au printemps et le taux de refroidissement à l'automne sont

pratiquement les mêmes à chacun des deux autres points. Cependant la température passe de 4.0 à 12.0 C en 44 jours à l'île d'Entrée et en 52 jours à Borden.

Le nombre de jours pendant lesquels la température à chaque station est plus élevée ou plus basse qu'un certain niveau peut servir à comparer les variations moyennes de températures à un certain nombre de stations. On peut voir, d'après les données du Tableau IV, des différences de milieu ambiant très grandes entre les stations situées dans le golfe même, d'une part, et celles établies en dehors du golfe, d'autre part, et aussi entre Grande-Rivière, l'île d'Entrée et Borden. Ces différences doivent avoir une influence énorme sur la vie pélagique à ces endroits.

Même si la glace du golfe Saint-Laurent n'apparaît pas toujours le long de la côte dans la région de Grande-Rivière, elle semble avoir une influence sur le réchauffement printanier des eaux de la région. L'année 1957 est typique à ce point de vue (Black, 1957). Ainsi lorsque la glace en hiver couvrait une grande partie du golfe comme, entre autres, en 1943, 1948, 1957, et 1961, la température

TABLEAU IV. Nombre de jours pendant lesquels la température de surface à certaines stations côtières est au-dessous ou au-dessus d'un niveau donné.

Station	Plus basse que 0 C	Plus basse que 4 C	Entre 4 et 12 C	Plus élevée que 12 C	Plus élevée que 16 C
Grande-Rivière	106	180	119	66	0
Île d'Entrée	101	167	103	95	43
Borden	97	153	86	126	79
Sambro Bateau-phare	0	109	141	115	34
St. Andrews	0	123	168	74	0

en mai était plus basse que la normale de 0.5 C en moyenne. Mais lorsque la glace était éparse comme, entre autres, en 1942, 1951, et 1958, la température en mai était de 0.4 C au-dessus de la normale. Un effet semblable mais plus prononcé se fait sentir aux Îles-de-la-Madeleine (île d'Entrée) et dans le détroit de Northumberland (Borden), où la glace est plus lente à disparaître.

L'écart des variations des températures mensuelles est en général plus élevé à l'île d'Entrée et à Borden qu'à Grande-Rivière, excepté pendant les mois de juillet et août. Les années froides ou chaudes à Borden et à l'île d'Entrée ne correspondent pas nécessairement aux même années qu'à Grande-Rivière. A l'île d'Entrée et à Borden, tout comme à Grande-Rivière, une année typiquement froide ou typiquement chaude est plutôt rare. Il arrive assez fréquemment qu'un printemps tardif (froid) soit suivi la même année par un automne tardif (chaud). On peut voir dans la Fig. 3 que les températures de l'eau de surface depuis mai jusqu'à août inclusivement étaient généralement basses en 1941, 1956, 1961, et 1962, et qu'elles étaient relativement élevées en 1942, 1951, 1952 (à l'exception de Borden), 1955 (à Grande-Rivière seulement), en 1959 et 1960 à l'exception de Grande-Rivière).

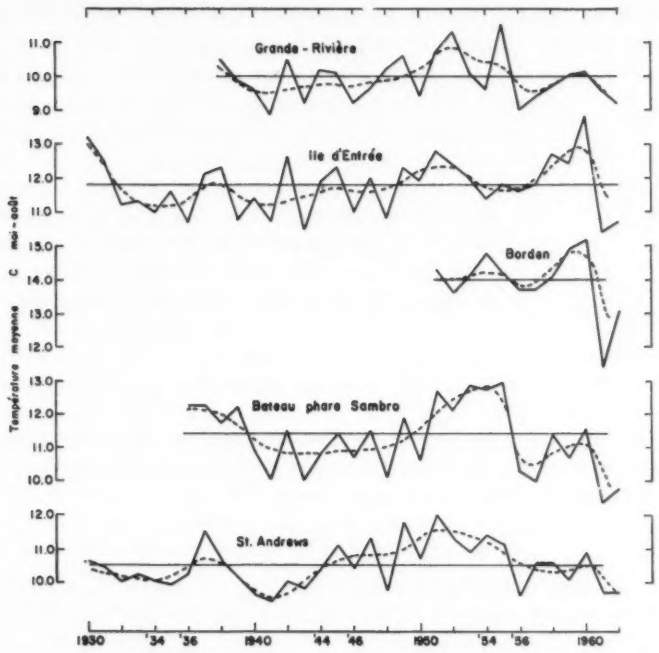

FIG. 3. Variation de la température, de mai à août, en fonction des années pour Grande-Rivière, île d'Entrée, Borden, Bateau-phare Sambro, et St. Andrews. La ligne pointillée est un tracé à main levée.

VARIATIONS À LONG TERME

Pour Grande-Rivière, ce sont les observations faites pendant les mois d'été qui s'étendent sur une plus longue période; on s'est servi de la moyenne des températures de mai à août inclusivement comme base d'étude des variations à long terme. Les résultats enregistrés pendant la même période (mai–août) à d'autres stations situées dans le golfe et même en dehors du golfe Saint-Laurent ont aussi été utilisés comme points de comparaison.

Les moyennes de températures de surface pour cette période de 4 mois, depuis 1930 jusqu'en 1962, font voir le niveau moyen des températures à chaque station, leur variabilité et surtout leur tendance ou leur variation à longue échéance. La Fig. 3 comprend les données provenant des observations faites à St. Andrews, N.-B. et au bateau-phare Sambro, stationné au large d'Halifax. La température moyenne de mai à août est de 10.0, 11.8, et 14.0 C pour Grande-Rivière, l'île d'Entrée, et Borden, respectivement, à comparer à 10.6 C pour St. Andrews et 11.4 C pour Sambro. Si l'on fait exception de la variation entre 1960 et 1961, on peut voir que la variabilité d'une année à l'autre dans le golfe est minimum à Borden; elle est approximativement la même à Grande-Rivière et à l'île d'Entrée. Le tracé de la variation moyenne

en fonction du temps, bien qu'approximatif, fait voir que les températures à toutes les stations étaient, au commencement de la décennie de 1940, celles d'une période généralement froide. Des années relativement chaudes durant la décennie de 1930 avaient fait place à des années froides au commencement de celle de 1940. Le réchauffement subséquent était sensiblement plus lent dans le golfe que dans les eaux au large de la Nouvelle-Écosse.

Une méthode plus rigoureuse de grouper les données est l'emploi d'une moyenne mobile pour une certaine période d'années. Des moyennes mobiles de 7 et de 10 ans ont déjà été calculées pour St. Andrews et d'autres points de la côte de l'est du Canada. La Fig. 4 fait voir ces moyennes pour Grande-Rivière, l'île d'Entrée, Borden, et St. Andrews. La similarité entre les variations à Grande-Rivière et St. Andrews est grande surtout pour les moyennes de 7 ans; elle est moindre pour la période de 10 ans. Les eaux à l'île d'Entrée semblent s'être réchauffées de 1940 à 1960, alors que celles de Grande-Rivière ont commencé à se refroidir après la période 1949–55. Les variations à longue échéance des eaux de la région de Grande-Rivière ressemblent beaucoup plus à celles des eaux en dehors du golfe Saint-Laurent que celles des eaux du plateau même des Îles-de-la-Madeleine.

DISCUSSION

Jusqu'ici nous avons signalé les variations de températures des eaux de surface d'une station côtière à l'autre, d'une année à l'autre, sans tenir compte de quelques-uns des facteurs responsables du réchauffement, soit l'échange de chaleur à la surface de la mer, l'échange de chaleur entre les nappes d'eau et l'apport de chaleur venant d'autres régions par les courants.

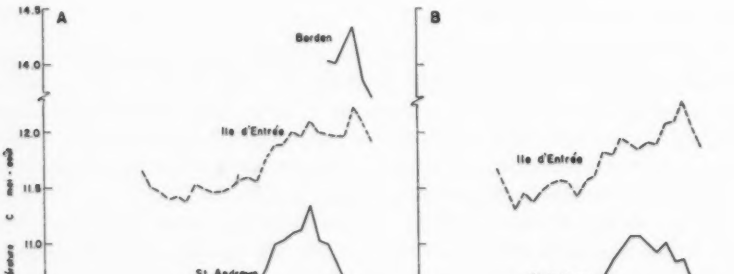

FIG. 4. Température mobile de 7 ans (A) et de 10 ans (B) attribuée à la dernière année de la période pour les différentes stations côtières.

Échange de chaleur à la surface

Nous n'avons pas de mesures exactes de la quantité de chaleur reçue ou émises à la surface de la mer dans cette partie du golfe Saint-Laurent. Cependant en utilisant des données océanographiques et météorologiques, nous avons calculé la quantité moyenne de chaleur reçue (après avoir soustrait celle qui a été émise), du mois d'avril au mois d'août, sur le plateau des Îles-de-la-Madeleine, entre l'île du Cap-Breton, et la Gaspésie. Ces calculs ont été faits seulement pour la période des années 1951–57. La variation de la température moyenne, de mai à août, à l'île d'Entrée semble liée étroitement à la quantité de chaleur reçue à la surface de la mer (Fig. 5); par contre il ne semble pas qu'on puisse établir une telle relation pour les eaux de surface à Grande-Rivière et à Borden.

Échange de chaleur entre les nappes d'eau

Les échanges entre les nappes d'eau sont largement influencés par la stabilité de la colonne d'eau dans cette région du golfe où les stratifications de la température et de la salinité sont prononcées. La stabilité de la colonne d'eau dans ces parages est fonction de l'apport d'eau de faible salinité venant de l'estuaire du Saint-Laurent et le minimum de salinité observé de juin à août, selon le lieu, est fonction de la décharge du Saint-Laurent (Lauzier, 1957a). Les variations saisonnières de la salinité dans le sud-ouest du golfe Saint-Laurent ont déjà été étudiées (Lauzier, 1957b). Les variations du minimum de salinité d'une année à l'autre, en un endroit donné, sont représentatives des variations du niveau estival de la salinité à l'ouest du chenal laurentien, entre la Gaspésie, et l'île du Cap-Breton. D'après les mesures de salinité faites depuis 1945 dans le secteur ouest de la région considérée, le minimum estival de la couche de surface a une valeur moyenne de 27.4‰, variant de 25.2 à 28.6‰. Une salinité relativement élevée en surface diminue le gradient vertical de salinité et la stabilité de la colonne d'eau, ce qui facilite les échanges thermiques entre les couches de surface et les couches inférieures. On peut s'attendre à rencontrer des températures estivales relativement basses en surface, résultant de l'échange de chaleur entre les différentes nappes d'eau, pendant les années où la salinité de surface est relativement élevée comme en 1946, 1956, 1957, et 1959. Par contre les températures sont relativement élevées en surface pendant les années de faible salinité comme en 1947, 1952, 1955, et 1960 (Tableau V).

Par comparaison avec les échanges de chaleur à la surface même, nous avons établi (Fig. 5) une relation entre la température moyenne à l'île d'Entrée et à Grande-Rivière, et le minimum estival de salinité aux mêmes endroits. On peut ainsi voir que cette relation semble plus significative pour les eaux de Grande-Rivière que pour celles de l'île d'Entrée et de Borden. Cela s'explique par le fait que les eaux avoisinantes sont plus profondes et plus stratifiées dans la région de la Gaspésie qu'aux Îles-de-la-Madeleine. A Borden, situé dans le secteur central étroit et peu profond du détroit de Northumberland, les eaux sont sujettes à un mélange assez prononcé dû aux marées. Ces conditions

réduisent la stabilité de la colonne d'eau même à l'entrée du détroit de Northumberland.

TABLEAU V. Température de surface pendant les années de forte et de faible salinité.

Station	Années	Température (*C*)			Salinité (‰)	
		Réchauffement de mai à août	Température moyenne de mai à août	Maximum en août	Minimum en juillet	Gradient vertical 0–20 m
Au large de l'Île-du-Prince-Édouard	1946, 56, 57, 59			17.7	28.2	0.9
	1947, 52, 55, 60			19.1	25.8	1.8
Grande-Rivière	1946, 56, 57, 59	8.1	9.4	13.9		
	1947, 52, 55, 60	10.2	10.6	14.8		
Île d'Entrée	1946, 56, 57, 59	11.8	11.7	16.8		
	1947, 52, 55, 60	12.4	12.5	18.0		
Borden	1956, 57, 59	11.0	14.1	18.5		
	1952, 55, 60	12.2	14.3	19.3		

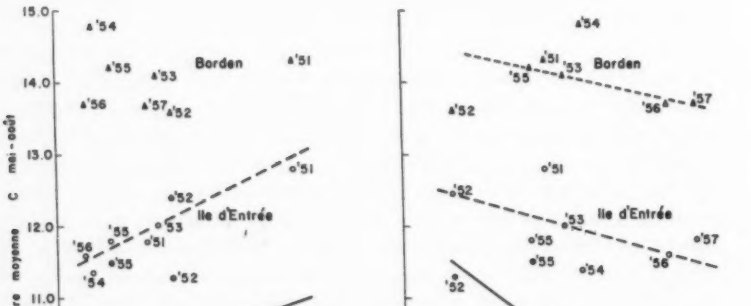

FIG. 5. Température moyenne, de mai à août, à Grande-Rivière, à l'île d'Entrée et à Borden en fonction de la salinité estivale moyenne et de l'énergie calorifique reçue à la surface de la mer sur le plateau des Îles-de-la-Madeleine.

Effet de la circulation

On peut aussi supposer que les eaux de la région de Grande-Rivière, étant à proximité du courant de Gaspé, sont rapidement renouvelées par des eaux fortement stratifiées, tandis que celles de la région des Îles-de-la-Madeleine, partie d'un élargissement du golfe Saint-Laurent, se déplacent plutôt lentement au-dessus d'un plateau peu profond. Ces eaux perdraient ainsi de leur stratification sous l'action des forces extérieures telles que le vent et seraient ainsi facilement sujettes à des échanges verticaux de chaleur, contrairement aux eaux de Grande-Rivière.

La recapture des bouteilles dérivantes libérées près de la côte de la Gaspésie dans la région de Grande-Rivière indiquent que les eaux de surface ont une forte tendance à s'éloigner vers le large. Sur quelque 270 bouteilles libérées en dehors de 10 milles des côtes, au cours de six croisières, 4% ont été retrouvées le long de la côte de la Gaspésie dont la plupart provenaient d'une seule croisière et 21% au sud et à l'est de la Gaspésie. Nous pouvons donc supposer que dans cette région un certain mouvement de montée des eaux froides des couches inférieures vers la surface accompagne le mouvement vers le large des eaux de surface.

Comme ces eaux proviennent probablement du segment côtier du courant de Gaspé, elles ont une salinité relativement basse par rapport aux eaux de la région des Îles-de-la-Madeleine; elles maintiennent près de la côte de la Gaspésie une stabilité relativement élevée. Ce phénomène semble être prédominant au printemps et au commencement de l'été.

Des trois facteurs considérés, la stratification et les courants semblent avoir une influence plus prononcée à Grande-Rivière qu'à l'île d'Entrée, l'échange ou l'absorption de chaleur à la surface de la mer étant le facteur prédominant à l'île d'Entrée.

Variations à long terme

Les eaux de Grande-Rivière et celles de l'île d'Entrée sont très différentes quant aux variations à long terme. D'une part les variations constatées à Grande-Rivière sont semblables à celles observées en dehors du golfe Saint-Laurent; d'autre part les variations observées à l'île d'Entrée sont pratiquement des phénomènes à caractère local, c'est-à-dire où les facteurs locaux, qui contrôlent le régime thermique des eaux, semblent masquer ou retarder les variations à long terme se produisant à d'autres endroits.

Jusqu'à quel point est-il possible d'expliquer la relation qui existe entre les variations à long terme à Grande-Rivière et en dehors du golfe Saint-Laurent ?

Les eaux profondes du chenal laurentien subissent des variations de température à long terme (Lauzier et Trites, 1958; Lauzier, 1964). Ces variations de température ressemblent dans une certaine mesure à celles des eaux couvrant le plateau continental (en dehors du golfe Saint-Laurent). Les eaux profondes du chenal laurentien en pénétrant en amont sont disponibles pour le mélange des eaux dans l'estuaire (Hachey *et al.*, 1956) et contribuent forcément à l'éta-

blissement du niveau de température des eaux de mélange qui descendent vers l'océan par le courant de Gaspé. Les variations de température dans les régions profondes de l'estuaire, de 1934 à 1957, sont aussi remarquables que dans le détroit de Cabot. Ainsi les eaux de la région de Grande-Rivière qui, dans une certaine mesure, subissent l'influence du courant de Gaspé, ont des propriétés thermiques liées indirectement à celles des eaux profondes du chenal laurentien. Il ne faut donc pas s'étonner de voir que les variations à long terme soient semblables dans la région de Grande-Rivière et en dehors du golfe. Par contre les propriétés thermiques des eaux des régions peu profondes du plateau des Îles-de-la-Madeleine comme celles de l'île d'Entrée sont modifiées localement au point que les variations à long terme diffèrent de celles des autres régions.

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Natural Infections of Cyclopid Copepods with Procercoids of *Triaenophorus* spp.[1]

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ABSTRACT

Sampling of the littoral and open water plankton from the spring of 1953 to 1959 established *Cyclops bicuspidatus thomasi* Forbes as the first intermediate host of *Triaenophorus* spp. in Heming Lake, Manitoba. Infection was apparently confined to a brood of *Cyclops* hatched in early May and maturing in mid July. The most heavily infected *Cyclops* were collected in the inshore areas. Inspection of a series of standard tows showed evidence of nonrandom distribution of infection, probably representing a clumping of the cyclopids. Implications of the uneven distribution for establishing infection rates, adequate sampling programs, and survival of the parasite are discussed.

INTRODUCTION

Few studies on level of infection of planktonic organisms with larval pseudophyllidean parasites have been published, either due to difficulties in identification and detection or the low levels of infection normally found. Percorini (1959) studied the spatial and temporal relations of several species of *Cyclops* and *Diaptomus* infected with a larval proteocephalid believed to be adult in whitefish and shad from Lake Maggiore. She found differences in the infection with time and locality and apparent decrease in number of eggs laid by infected females. Miller (1943) surveyed Lesser Slave Lake plankton for intermediate hosts of *Triaenophorus*, but not on a quantitative basis.

This paper discusses the results of 7 years' sampling of the littoral plankton of Heming Lake, Manitoba, the site of a *Triaenophorus* control experiment conducted by the Fisheries Research Board of Canada. *Triaenophorus crassus* Forel, *T. nodulosus* (Pallas) (= *T. lucii* Müller) and *T. stizostedionis* Miller were found in the lake, but during most of the study there was a preponderance of adult *T. nodulosus* in the gut of its final host the pike, *Esox lucius* Linnaeus. Numbers of *Triaenophorus crassus* were declining in pike and *T. stizostedionis* in walleye, *Stizostedion vitreum*, was rare. As far as the authors are aware, these species of pseudophyllidean tapeworms were the only ones present in animals frequenting the lake and producing larval stages infecting cyclopid copepods at the particular time of the year when samples were collected. Thus it seems likely that most of the procercoids observed were *Triaenophorus* probably *T. nodulosus*.

Miller (1952) reviews evidence that the eggs of *Triaenophorus* spp. are shed over a short period of time in the spring, and this seems true at Heming

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J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

Lake also. It is possible therefore to pinpoint the time when infected copepods would be present to the time of the study.

SAMPLING AREAS

Several areas, which had previously been shown by netting or angling to be frequented by pike infected with mature *Triaenophorus*, were selected for plankton sampling. Three of these, situated along the western shore of the lake in shallow, sandy-bottomed reaches of shoreline, were designated Heming Bay, Cabin Bay, and Bulrush Bay.

The shoreline in these areas is mostly lined with rocks and the water's edge is overhung with a heavy growth of alder, *Alnus rugosa*, sweet gale, *Myrica gale*, and heaths. Little or no wave-washed sandy shoreline has developed and the water is 10–15 cm deep under the overhanging shrubs and rocks at the shore.

In each of the three shore areas, there was a growth of rooted emergent and floating aquatic vegetation which grows rapidly in spring and early summer. The extent of this aquatic vegetation and its specific makeup varied somewhat from area to area, but the major species of plants common to all three areas includes bulrush, *Scirpus validus*, reed grass, *Phragmites communis*, horsetail, *Equisetum* spp., waterlilies, *Nuphar variegatum* and *N. microphyllum*, and *Potamogeton* spp.

Samples of plankton were also taken on the temporary flood-plain of the main inlet creek of the lake. It was a semi-solid sedge meadow which flooded 15–45 cm deep for about a month or more after breakup each spring. Samples from a shallow pool at the mouth of the creek were also taken as representing part of this habitat. These samples were designated Heming Creek Marsh and Heming Creek Mouth, respectively.

Surface tows, designated open-water tows, were taken from the middle of the lake in 3–5 m of water as a control to determine whether infection rate of the cyclopids from the littoral areas was characteristic of that of the whole lake.

COLLECTION AND EXAMINATION OF SAMPLES

Samples were made by pulling a Wisconsin-type tow net of #20 bolting silk behind a motor boat for a standard distance of 100 m in each of the two shore areas. These tows were made at the surface in about 1 m of water about 5 m from shore. The speed of the boat was adjusted to the straining efficiency of the net so that samples were taken at the surface of the water. The open-water tows were taken in a similar fashion.

In 1957 and later years, additional samples were taken at an intermediate distance from shore by wading through the water with the net and at the shore by scooping nets under the shore vegetation. Samples from the marsh area and at the creek mouth were also taken in this manner. Infection levels were difficult to obtain using this method because of the scarcity of animals in the samples.

Nets damaged by snags or clogged meshes were replaced during the sampling season.

Samples of plankton were examined alive. Experience proved that this method gave much better visibility of internal organs and cavities of the *Cyclops* than with preserved animals, which had to be cleared by a variety of techniques. The motion of procercoids in living or narcotized animals helped in spotting infections. When the samples could not be examined immediately after collection, excess debris such as decaying vegetation or pine pollen was removed to reduce the oxygen consumption. These samples were stored for a maximum of 2–3 days at temperatures between 5 and 10 C.

Samples were concentrated and examined in a Sedgewick-Rafter counting cell after immobilization by ethanol. The low power (10 ×) of a compound microscope gave sufficient magnification for identification of copepodite and adult stages of the cyclopids in the tows, and proved adequate for the detection of the procercoids. It was impossible to be certain whether a few of the *Cyclops* were infected or not, as they contained dark yolky egg-masses or were oriented in an unfavorable manner for observation. Such individuals made up only a small proportion of the total and were not counted. For each sample, the number of infected and noninfected cyclopids, the general species composition of the sample, the maturity of the majority of the animals, and the presence of other parasite forms was recorded.

Several species of copepods listed by Lawler and Watson (1958) were found in the tows. The most frequently occurring species of cyclopids from the open water and standard shore tows were *Cyclops* (*Diacyclops*) *bicuspidatus thomasi*, *C.* (*Acanthocyclops*) *vernalis brevispinosus* and *Mesocyclops edax*. Proportions of each species varied during the season, but *C. b. thomasi* was more abundant in the early part of the sampling period and *C. v. brevispinosus* was more abundant by July. In the shallower Heming Bay tows, and in scoops from the shoreline, especially as the water became warmer and somewhat weedy, *Tropocyclops prasinus* and *Eucyclops agilis* were sometimes numerous, almost replacing *C. b. thomasi* and to a lesser degree *C. v. brevispinosus*. The creek marsh and creek mouth had a different cyclopid fauna. The most numerous species here were *Macrocyclops albidus*, *M. fuscus*, *Eucyclops agilis*, *Paracyclops fimbriatus poppei*, an unidentified subspecies[3] of *C. vernalis* and *C.* (*Microcyclops*) *varicans rubellus*. These species of cyclopids were examined for natural infections, as they had been proven capable of experimental infection (Watson and Price, 1960). *Diaptomus oregonensis*, *D. minutus*, *Epischura nevadensis* and *E. lacustris*, when present in tows, were also routinely examined for procercoid larvae.

RESULTS

Of this assemblage of copepods, only *C. b. thomasi* and *C. v. brevispinosus* were found infected with *Triaenophorus*. Over the years some 30,000 of each of these species were examined. All the infections noted were in *C. b. thomasi*

[3]In this paper we differ somewhat from Price (1958) in referring his "reproductive isolates" of *C. vernalis* Fischer to subspecies rather than separate species.

except for three in *C. b. brevispinosus*, so that *C. b. thomasi* must be considered the only important natural host of *Triaenophorus* in Heming Lake. This is the same as for Lesser Slave Lake, Alberta (Miller, 1943). In any locality in any year about 1 or 2% of *Cyclops bicuspidatus thomasi* were infected (Table I).

A higher proportion of infected plankters was in shore tows than in tows at the centre of the lake (Table I). Infection observed in the "open water" tows was negligible. In the later years of the study, shore samples and tows at an intermediate distance from shore in Cabin Bay and Heming Bay yielded infection rates decreasing more or less regularly with distance from the shore. Scoop samples from the pool off the creek mouth were as heavily infected as the shore scoops. In a scoop of 85 individuals from Cabin Bay shore on July 3, 1959, 80 were infected. This high degree of infection was not duplicated or approached in subsequent samples and points out some of the difficulties in getting adequate samples and reproducible results. Tows at an intermediate distance from shore were less frequent, but average infection rates lie between the standard tows and the shore scoops. No *C. b. thomasi* (and no infection) were observed on the creek marsh. There was no noticeable difference between the infection of shore scoops or standard tows at the three localities.

Some infected individuals were observed at the onset of sampling in mid May. However, possibly as a result of increased size of the procercoids, most of the infected animals were observed in the second half of June (Fig. 1). Incidence of infection rapidly fell and no infected *Cyclops* were found after mid July. This can be directly related to the life cycle of the hosts.

Sampling at the time when the ice was breaking up around the shores (early May) yielded many adult female *C. b. thomasi*, none of which was infected. These apparently died after laying several batches of eggs. It was possible to follow the procercoids only through this brood of *Cyclops*. By mid May procercoids were found in those which had developed to the second or third copepodite stage. Development was arrested at the fourth copepodite stage through most of June. Some fifth copepodite stage and adult individuals were found in late June and early July, after which time *C. b. thomasi* disappeared from the littoral and surface plankton samples, and no further infection was found.

A few other larval parasites were noted in the copepods. These included larval nematodes in *Mesocyclops edax*, *C. b. thomasi*, and *C. v. brevispinosus*, large procercoids probably of *Diphyllobothrium* in *Diaptomus* and hymenolipid cysticercoids in *Ephischura*. Most of these parasites were found each year, generally towards the end of the sampling season, and no effort was made to assess their incidence or distribution in the lake.

DISCUSSION

This study indicates that infections with *Triaenophorus* at Heming Lake take place in one generation of *Cyclops bicuspidatus thomasi*. Elgmork (1959) described a similar life cycle for *Cyclops strenuus strenuus* in small Norwegian lakes, with the complication that varying proportions descend to the sediments

TABLE I. Number of *Cyclops bicuspidatus thomasi* examined each season in each location and number infected with *Triaenophorus* spp.

	1953		1954		1955		1956		1957		1958		1959	
Location	Exam.	Inf.	Exam.	Inf.	Exam.	Inf.	Exam.	Inf.	Exam.	Inf.	Exam.	Inf.	Exam.	Inf.
						I. Standard tows								
Cabin Bay	2220	30	3110	56	1976	6	2241	6	4740	8	2527	5	1097	20
Heming Bay	2933	71	2280	31	1975	11	1994	12	4850	9	1143	0	606	11
Bulrush Bay	...	...	1486	11	2110	13	1887	4	3211	4	609	0	...	...
						II. Tows an intermediate distance from shore								
Cabin Bay	...	...	...	...	...	...	...	...	1484	3	347	6	241	1
Heming Bay	...	...	...	...	...	...	...	...	...	...	110	0	208	4
						III. Shore scoops								
Cabin Bay	...	...	...	...	...	...	...	...	2304	10	937	1	242	84[a]
Heming Bay	...	...	...	...	...	...	...	...	2696	36	537	0	77	0
Heming Creek Mouth	...	...	...	...	...	...	272	30	1148	1	146	3	608	44
						IV. Open-water tows								
Station #2	585	3	800	5	158	0	...	...	9984	5	3681	0	1428	0

[a]Includes one sample of 80 infected *Cyclops* out of 85 present.

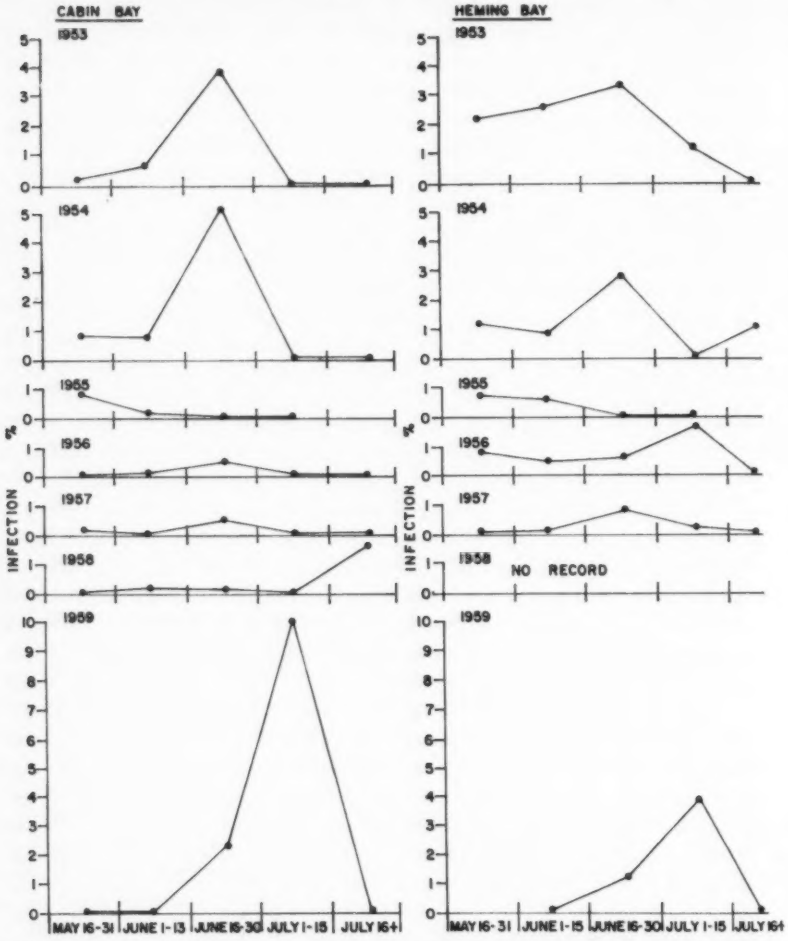

FIG. 1. Annual incidence of *Triaenophorus* spp. (per cent) in *Cyclops bicuspidatus thomasi* from two shallow-water regions of Heming Lake, Manitoba.

and pass the summer in a dormant condition in the IV copepodite stage. Cole (1955) and others described a similar resting stage in certain populations of *C. b. thomasi*. If all the *Cyclops* of this brood matured and died by mid July, the period of time each year when infective larvae of *Triaenophorus* were available to susceptible small coregonines or other small fish which act as second intermediate hosts would be limited. Preliminary investigations did not reveal any quiescent copepods in a few mud samples examined at Heming Lake, but their presence and possible importance in the life cycle of *Triaenophorus* should not be overlooked.

It is possible, but not proven, that procercoids can survive in resting *Cyclops* over the summer months. The question must be answered in order to determine the length of time infection is present in the lake.

The distribution of infected *Cyclops* was not uniform over the whole lake. Individuals in the open water plankton appeared to have a very small chance of being infected and the majority of infection was found within 20 ft from shore. To further determine the homogeneity of infection in these inshore *Cyclops* populations, samples from Cabin Bay and Heming Bay were compared with respect to the frequency of infection. With such low infection rates, the majority of samples had no infected animals. The next most frequent categories were those with one and two infected animals. Very few samples contained five or more infected individuals (Table II).

TABLE II. Annual incidence of *Triaenophorus* spp. in samples of *Cyclops bicuspidatus thomasi* (Cabin Bay and Heming Bay standard tows combined).

Infected *Cyclops* per sample	Number of samples per year						
	1953	1954	1955	1956	1957	1958	1959
0	21	79	50	84	98	60	38
1	8	15	13	11	6	2	8
2	7	7	3	3	0	1	0
3	3	4	0	0	1	0	0
4	1	2	0	0	0	0	2
5 or more	4	4	0	0	1	0	1
Total number of samples	44	111	66	98	106	63	49
Mean number of infected *Cyclops* per sample	1.36	0.75	0.30	0.17	0.13	0.06	0.43

Infection per sample of shore scoops and of intermediate distance tows was higher than that of standard tows, but irregularities in the sampling data preclude a similar treatment for them.

The distribution of samples in Table II suggested the type found from clumped aggregations (Andrewartha, 1961). Although insufficient for statistical treatment, consistently more samples with zero infections and less with one than would be expected had the samples been drawn from a Poisson series indicating some clumping.

From this evidence, it was evident that the infected *Cyclops* were not distributed uniformly or randomly in the surface plankton of the lake. Greater concentrations are found close to shore in shallow water than in the centre of the lake.

Since there was evidence for nonrandomness of distribution in infected *Cyclops*, and particularly because seasonal totals represented subsamples from one generation of *Cyclops* which had passed through one infection period, infection rates determined for each area in each year of the study probably represented a relative rather than an absolute measure of infection.

This study demonstrated some of the difficulties inherent in any quantitative study of the plankton populations. It is apparent that, in order to be at all accurate, a study of natural rates of infection of planktonic organisms in a lake must include studies of life cycles and movements of the host organisms.

The nonrandom type distribution of infected *Cyclops* in the plankton of the lake is important from several points of view. It is possible that the apparent clumping of infection may represent swarms of plankton organisms. Several workers, including Fraser (1960) and Hopkins (1959) who studied dynamics of cestode infections, tried to explain the discrepancy between overall infection rates of copepods, known feeding habits and capacity of the fish, and observed rates of infection in the fish. Generally, in such studies as these, infection levels in the copepod intermediate host are much lower than expected from the level of infection observed in the fish. Clumping of the copepod hosts and especially aggregations of infected animals in littoral areas of the lake system undoubtedly would increase the chance of infection of the second intermediate host. A concentration of infected first intermediate hosts in a limited area of the lake would favour encounters with the second intermediate host and must enhance the chances that the life cycle will be completed. It also seems likely that such clumping of the infected plankton would result in either zero or multiple infections in the second intermediate hosts.

ACKNOWLEDGMENTS

Samples were collected and examined by Messrs A. B. McBurney, R. R. Wheaton, C. D. O. Foster, and others. Comments and criticisms of Dr G. F. M. Smith, Fisheries Research Board of Canada, and Mr W. J. Christie, Ontario Department of Lands and Forests, during the preparation of the manuscript are gratefully acknowledged.

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Lymphocystis Disease in American Plaice of the Eastern Grand Bank[1]

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ABSTRACT

Lymphocystis infection is described and figured, both for gross appearance and for microscopic sections of American plaice, *Hippoglossoides platessoides* (Fabricius), from the eastern slope of the Grand Bank. This infection was first noticed in American plaice from this area in September 1960. Between July and early October 1964 about 1% of the American plaice of commercial size caught on the southern part of the eastern slope of the Grand Bank showed lymphocystis nodules, usually between 0.6 and 2.0 mm diameter, on the surface of the skin, on the upper and lower surfaces and on the fins, either separate or in tumours made up of individual nodules surrounded by connective tissue and covered externally by epidermis.

INTRODUCTION

Brief review of the Development of Knowledge of the Nature of the Lymphocystis Infection

Lowe (1874) made the first apparent reference to an infection, similar to that later called lymphocystis disease, in the skin of the European flounder, *Pleuronectes flesus*, of the Norfolk area. Additional references to this disease in flounders and also in the plaice, *Pleuronectes platessa*, were made by McIntosh (1885, 1886). Sandeman (1893) gave a more detailed description of the lymphocystis nodules or tumours of the flounder: as individual white spheres 1–1.5 mm in diameter situated just below the pigmented layer of the epidermis, and larger tumours composed of numerous individual tumours similar to the smaller individual nodules. Woodcock (1904) dealt in more detail with the internal structure of the lymphocystis nodules or as he called them parasites. He provided a good figure of both individual nodules and composite lymphocystis tumours on the anterior part of a flounder and also individual nodules in the mesenteries of the intestine. Woodcock believed that each individual nodule was a sporozoan parasite and gave it the name *Lymphocystis johnstonei*. Johnstone (1905, 1907) also described *Lymphocystis johnstonei* in the flounder and in the sole, presumably *Solea vulgaris*. Subsequent investigators, although some were doubtful, followed the idea that these small tumours were individual parasites, until this idea was supplemented by the view first developed by Weissenberg (1914) that these small lymphocystis nodules or giant cells were greatly hypertrophied and transformed connective tissue cells.

Mavor and Feinberg (1918) first reported lymphocystis disease in America, in the walleye or pike-perch, *Stizostedion vitreum*, in Wisconsin. They considered

[1]Received for publication March 23, 1965.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

the infection to be caused by a sporozoan of the same general type as *Lymphocystis johnstonei* but, believing it to be different, gave the name of *Lymphocystis vitrel* to the parasite of *Stizostedion*.

Weissenberg (1914, 1921b) showed for *Pleuronectes flesus* and the European perch of the Baltic, *Acerina cernua*, that healthy fish were readily infected with lymphocystis when kept in the same water with lymphocystis-infected individuals of their own species. Weissenberg (1920–1951b) also developed the view that the lymphocystis hypertrophy of the connective tissue cells is caused by an intracellular virus. This view was soon adopted by other authors.

Rašín (1927, 1928) produced lymphocystis disease in the paradise fish, *Macropodus* sp., by bathing a specimen with the skin damaged over an area by removal of scales, in water containing a suspension made from lymphocystis nodules. A dilution of 1 in 1 million was still virulent. Lymphocystis nodules occurred at the site of the infection. The susceptibility of the fish was increased by applying the virus directly to the damaged skin. Viral material 105 days old proved infective. Nodules of lymphocystis 105 days old after drying for 67 days over caustic potash sticks at 18–20 C were still infective but with greatly diminished virulence. Rašín considered that the lymphocystis-infected flounders reported by Weissenberg probably became infected through the skin as a result of burrowing in the sand, rather than through the gills. As the fins are the most easily damaged parts they are the most readily infected. Apparently, however, Weissenberg has not changed his belief that lymphocystis disease is transmitted through the gills (Nigrelli, 1952). Presumably the parasite could enter most readily through any injured or easily penetrated area. Infection in nature is presumed to occur either through lymphocystis cells or virus transmitted by the water or by ectoparasites. In this connection Nigrelli (1950, 1952) reported that the degree of infection with lymphocystis was apparently correlated with the degree of infection of the gills with ergasilid copepod parasites and that the reproductive cycles of these copepods coincided with the appearance of the disease.

In the walleye the incidence of lymphocystis disease among marked fish was more than three times that of the unmarked fish. Lymphocystis tumours were often present in the area where scale samples had been taken and on the stub of the clipped fin (Ólsen, 1958). In the walleyes of the Nipigon River lymphocystis was at a high level only during and immediately after the spring spawning period. Lymphocystis may have resulted from the congestion on the spawning grounds and the removal of the mucous covering of the walleyes in the shallow riffles of the spawning areas (Ryder, 1961).

Weissenberg (1951a) produced evidence of the filterability of the lymphocystis virus by infecting a healthy *Fundulus* with bacteria-free filtered material from lymphocystis tumours of *Stizostedion*.

Wolf (1962), using mainly the bluegill, *Lepomis macrochirus*, transmitted lymphocystis disease by implantation and by injection. He could find no evidence of transmission of the infection between fishes living in the same water but treatment for ectoparasite control may have been a factor in this

result. The agent of the disease was propagated under laboratory conditions for more than 2 years. The host could be infected after passage of the infective agent through a fine filter, after storage at −20 C for 20 months and after desiccation.

Lymphocystis Disease

The present view is that lymphocystis is a viral and infectious disease of freshwater and marine fishes in which connective cells, fibroblasts, osteoblasts, etc., under the influence of the virus grow to an abnormally great size. These enlarged cells make up lymphocystis tumours which may be few or numerous small disseminated nodules or groups of nodules of individual lymphocystis cells or larger composite nodules or tumours usually on the skin and fins of fishes. When the individual nodules combine they generally show their composite structure superficially and when the resulting tumours are sectioned they are shown to be made up of individual nodules surrounded by connective tissue and covered externally by epidermis. Although occurring especially in the lymph spaces of the skin, these giant cells also occur in internal organs, mesentery, intestine, ovary, and spleen (Weissenberg, 1920, 1945; Nigrelli and Smith, 1939; Alexandrowicz, 1951; Nigrelli, 1952, 1954; Watson, 1954).

These giant lymphocystis cells, from an original diameter of 10–15 μ, may reach a diameter of 1–1.5 mm in the flounder, *Pleuronectes flesus* (Sandeman, 1893; Plehn, 1924) and in some fishes an even larger diameter of 5 mm (5000 μ) or more (Nigrelli, 1952; Watson, 1954).

The structure and development of the lymphocystis cell in various fishes have been discussed in detail by the following and other authors: Woodcock (1904), Joseph (1918), Weissenberg (1920, 1938, 1939b, 1945, 1951b), Weissenberg *et al.* (1937), Nigrelli and Smith (1939), Nigrelli (1952), and Alexandrowicz (1951).

Inclusion bodies are a notable feature of the cytoplasm of lymphocystis cells. These inclusion bodies are composed of material which stains like basichromatin. Although appearing as individual bodies, strings, or chains in the sections they are usually visualized in the complete cell to be in the form of a complex single network or groups of networks. The inclusion network may be near and sometimes surrounding the nucleus as in walleye, *Stizostedion vitreum* (Weissenberg, 1939b). In some fish it is close to the cell wall as in the red mullet, *Mullus surmuletus* (Alexandrowicz, 1951), and in other fish a network densely filling the whole cytoplasm as in the European flounder, *Pleuronectes flesus* (Weissenberg, 1920). Nigrelli and Smith (1939), for the orange filefish, *Alutera* (*Ceratacanthus*) *schoepfi*, found the inclusion bodies to be frequently dispersed in the region of the periphery of the cell and of the nucleus either as a network or as isolated granules.

Lymphocystis disease is usually not fatal. On specimens of the common sunfish, *Lepomis gibbosus*, and the bluegill, *Lepomis macrochirus*, kept in laboratory aquaria, Weissenberg (1945) observed that the whole course of the

disease took only 16–18 weeks. The tumours became visible to the naked eye in about 6 weeks after infection and reached their full size about 12 weeks after infection. By about 6 weeks after this time the lymphocystis cells had been lost.

Uninfected walleyes, *Stizostedion vitreum vitreum*, in Saginaw Bay weighed 5½–6½% more than infected fish of the same length (Hile, 1954). Infected white crappies, *Pomoxis annularis*, from Missouri weighed 3–5% less than sound fish of the same length (Witt, 1957).

In freshwater fish populations of temperate climates the disease usually appears in spring, develops to its greatest degree during summer and gradually disappears in fall and winter (Nigrelli, 1952, 1954; Watson, 1954). In the Philadelphia Aquarium, however, where the water was slightly warmed, epidemics in *Lepomis gibbosus* and *Lepomis macrochirus* occurred in the winter and disappeared by May (Weissenberg, 1945). In the white crappie in the Lake of the Ozarks, Missouri, the incidence of the disease was highest in July and August, decreased over winter and was lowest in April, after which it increased again (Witt, 1957).

In Sandeman's (1893) description of lymphocystis infection in plaice and flounders the tumours were present during the whole year but occurred principally in May to November, giving the infected fish an emaciated appearance. The flounders with lymphocystis infection examined by Woodcock (1904) showed no emaciation. The enlarged infected cells or tumours eventually disappear and the skin resumes a normal appearance.

In the flounder, *Pleuronectes flesus*, of the Öresund, in areas of high infection the percentage infected was higher in the two periods April–May and July–September, 7% and 10–12% in two areas, and lower in October–December and January–March, 3–4% and 7–8% in the same two areas (Nordenberg, 1962).

Lymphocystis disease has been reported for a few marine fishes from the Atlantic coast of the United States: the West Indian angelfish, *Angelichthys isabelita*, by Smith and Nigrelli (1937); the hogfish, *Lachniolaimus maximus*, by Weissenberg *et al.* (1937); the orange filefish, *Alutera schoepfi*, by Weissenberg (1938); and for the common killifish, *Fundulus heteroclitus*, by Weissenberg (1939a). Nigrelli (1952) shows lymphocystis tumours on a West Indian cowfish, *Lactophrys tricornis*, from the west coast of Florida and says that he has studied lymphocystis infections in several additional marine fishes in the Atlantic, including the striped bass, *Roccus saxatilis*, from New York and Connecticut coastal waters. Nigrelli (1954) lists species, locality, and author references to the occurrence of lymphocystis disease in North American temperate freshwater fishes.

Although lymphocystis disease is common in the European flounder, occurs also in the European plaice, and has been recorded in the European sole, there appears to be no reference to its occurrence in the American plaice, *Hippoglossoides platessoides*, or in the same species known in Europe as the

long rough dab (but possibly a different subspecies), and often but not always given a different generic name, *Drepanopsetta platessoides*. Also we have found no reference to the occurrence of lymphocystis in any pleuronectid of the western Atlantic nor for any marine fish of the eastern Canadian area.

Only a brief review of some of the more important aspects of lymphocystis infection can be given here. For further details on the history, histology, experimental background, and life history of the pathogen and its hosts see Weissenberg (1920), Nigrelli and Smith (1939), Nigrelli (1952), and Alexandrowicz (1951).

OCCURRENCE OF LYMPHOCYSTIS DISEASE IN AMERICAN PLAICE

Gross Description

On September 19, 1960, 28 American plaice with a nodular infection of the skin, caught by the St. John's trawler *Blue Haze* on the eastern Grand Bank, were brought to the St. John's Station and examined by the author. Additional American plaice with similar infections of the skin were obtained in 1961 and especially in 1964.

In August 1963 portions of skin containing these nodules obtained in 1960–61 were sent to Dr Z. Kabata of the Marine Laboratory, Aberdeen, who examined them and wrote on August 20, 1963 that these nodules from *Hippoglossoides platessoides* provide an excellent example of lymphocystis which is particularly frequent on flatfishes but he knows of no previous record of lymphocystis on the long rough dab.

The small nodules, or individual giant cells were mainly between 0.6 and 2.0 mm in diameter and were in the connective tissue underneath the epidermis but outside the tough fibrous base of the skin. In some fish most of the nodules were in the upper half of this size range, in others mainly in the lower half or in the middle part of the range. Although from a superficial examination some of the infected fish appeared to be in very bad shape, usually on scraping the skin no gross trace of the infection remained on the fleshy part of the body. The infection occurred on the upper or lower surfaces or on both, on the head often along the lower jaw and in front of the eyes, and on one or more of the dorsal, anal, caudal, and other fins.

Because this is the first description of lymphocystis disease in the American plaice and pictures are more descriptive than words, a variety of figures of American plaice is presented (Fig. 1–10) to show the pattern of some of the most severe lymphocystis infections encountered.

In some cases most of the giant lymphocystis cells are separate, though usually grouped, at the surface of the skin of either the upper or lower surface or both (Fig. 1, 2, 8). This is the condition that leads to the fishermen's name of seedy flounders. On the whitish lower surface, where there is no pigment interference, the lymphocystis cells (one-cell tumours) appear as pearly-white and are readily apparent (Fig. 1, 8). On the upper surface the lymphocystis

cells lie below the dark shield of the melanophores and the individual giant cells are usually not so visible (Fig. 2).

In other American plaice, and more unusually, most of the lymphocystis cells are grouped in small to large tumours (Fig. 3, 4). This suggests the name of scabby flounder which is used by some fishermen.

Another type, which is very common in cases of heavy infection, has a combination of both conditions, having large numbers of single lymphocystis cells, often closely grouped, and also small to large tumours containing from a few to many hundreds of lymphocystis cells (Fig. 5–7).

The small individual tumours (giant cells) may occur anywhere. They may be mainly on the surface of the body with extensions of the infection to the fins (Fig. 1, 8), or more usually over the surface of both body and fins (Fig. 2, 5, 6), or mainly on and at the bases of the fins (Fig. 7). The caudal fin may have a heavy infection (Fig. 2, 5).

Although medium-sized composite tumours containing a number of lymphocystis cells may be found over the surface of the body (Fig. 3, 4) the largest tumours that we have noted, containing many hundreds of lymphocystis cells, and the largest associated groups of smaller tumours usually occur on the fins (Fig. 5–7, 9B, 10) or near the edge of the body in front of the anal and sometimes in front of the ventrals (Fig. 9A).

A common location for a lymphocystis tumour in a heavily infected American plaice is behind the anus immediately in front of the anal fin. In this location are the largest tumours with the thickest covering (Fig. 3–5, 9A). Smaller tumours in this area may be seen in Fig. 2, 6, and 7. Johnstone (1905) figures and discusses a tumour found in this position on the European flounder, *Pleuronectes flesus*, and suggests that it may be due to the infection of a wound or skin abrasion caused by the sharp anal spine which projects forward at the anterior end of the anal fin but is normally covered with skin.

When the infection in the fins is great enough the lymphocystis tumour may be visible from both upper and lower sides of the fish (see Fig. 6 and 7 for the same large tumours visible on both sides on the anal fin (also Fig. 10) and toward the anterior on the dorsal fin).

Investigators have found that lymphocystis infections in some other fishes disappear, leaving reasonably normal skin conditions. It is, however, difficult to imagine that conditions after recovery at the site of the heavy infection of the dorsal fin in Fig. 5 and 6 and of the caudal fins of Fig. 2 and 5 would not leave some evidence of the former infection. Caudal fins with heavy infection appear ragged at the tips and irregular in outline but whether this is disease or deck and icing attrition has not been determined.

The surfaces of the viscera, mesenteries, and body cavities were examined in almost all the American plaice received at the Station with lymphocystis infections of the skin and no lymphocystis nodules were found.

We have not found copepod parasites on the gills or fins of the American plaice infected with lymphocystis nor did the fish appear to be emaciated.

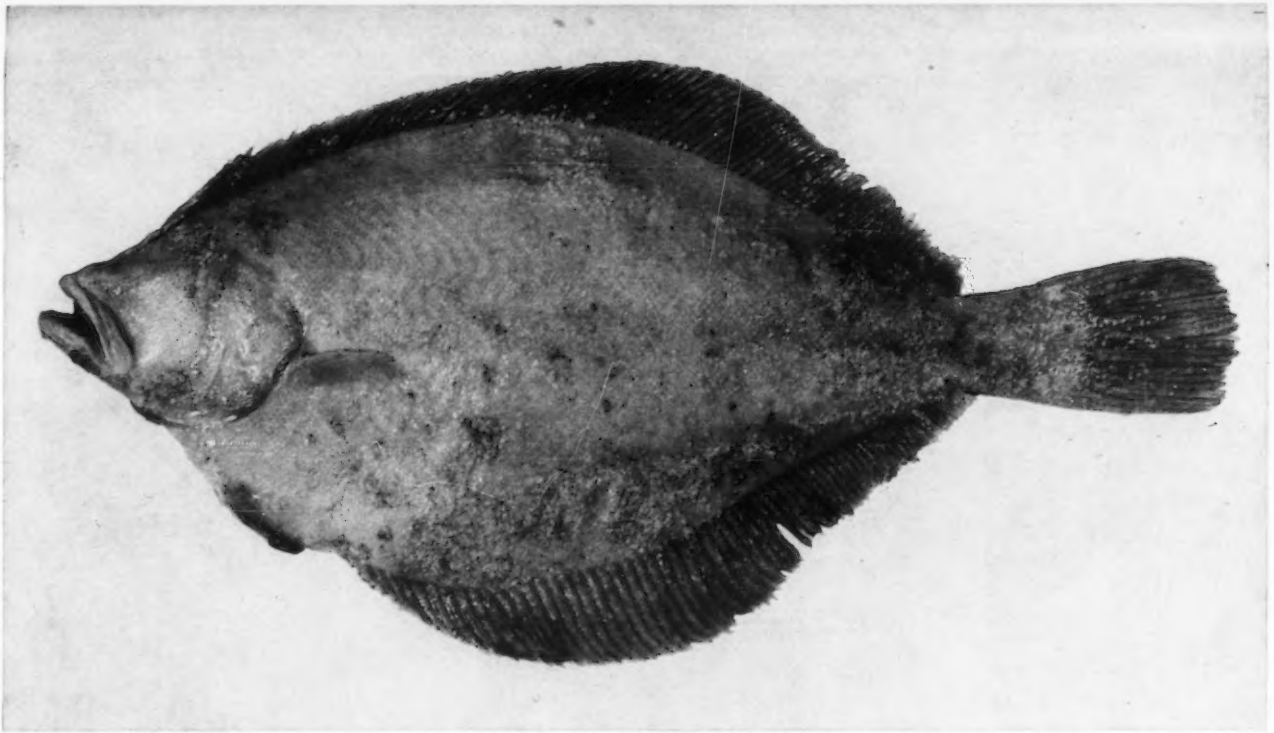

FIG. 1. Lymphocystis infection on the left (lower) side of an American plaice, 53 cm, female mature, taken by the trawler *Blue Spray*, August 1–8, 1964, on the eastern slope of the Grand Bank, 43°10′N–45°35′N, 80–220 m. (Shows mainly individual lymphocystis cells. In this and in Fig. 2–7 which are less than half natural length, a hand lens will be useful in studying the infection.)

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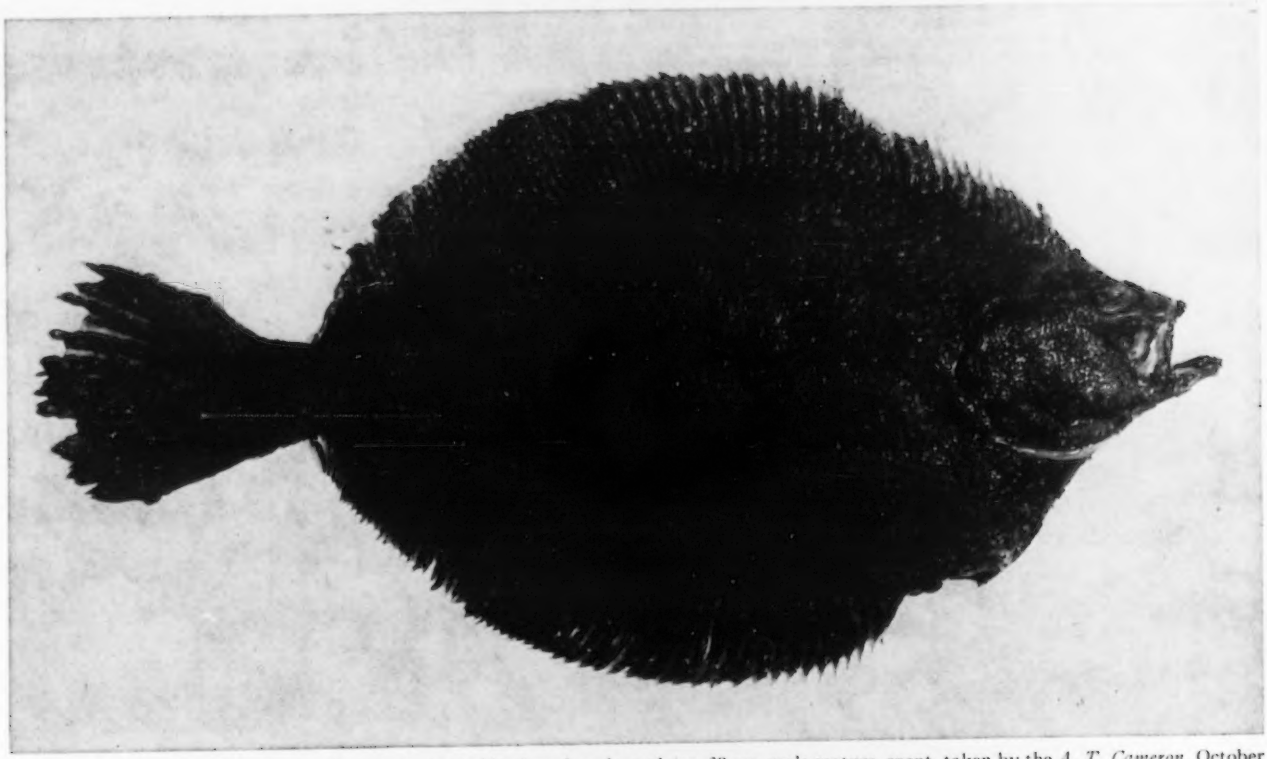

FIG. 2. Lymphocystis infection on the right (upper) side of an American plaice, 39 cm, male mature, spent, taken by the *A. T. Cameron*, October 2–11, 1964, on the eastern slope of the Grand Bank, 44°58′N–45°06′N, 100–180 m. (Shows mainly individual lymphocystis cells.)

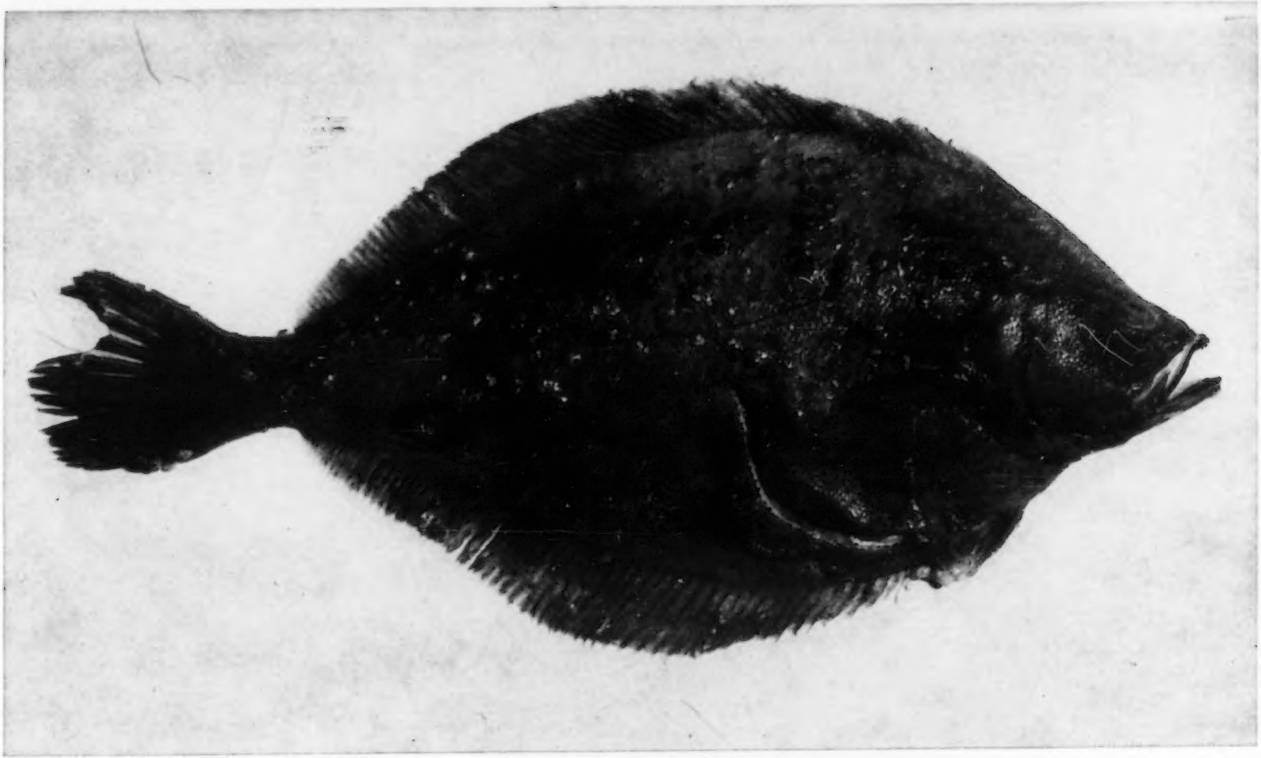

FIG. 3. Lymphocystis infection on the right (upper) side of an American plaice, 47 cm, female mature, spent. (Ship, date, location, depth as in Fig. 2. Shows small tumours composed of lymphocystis cells.)

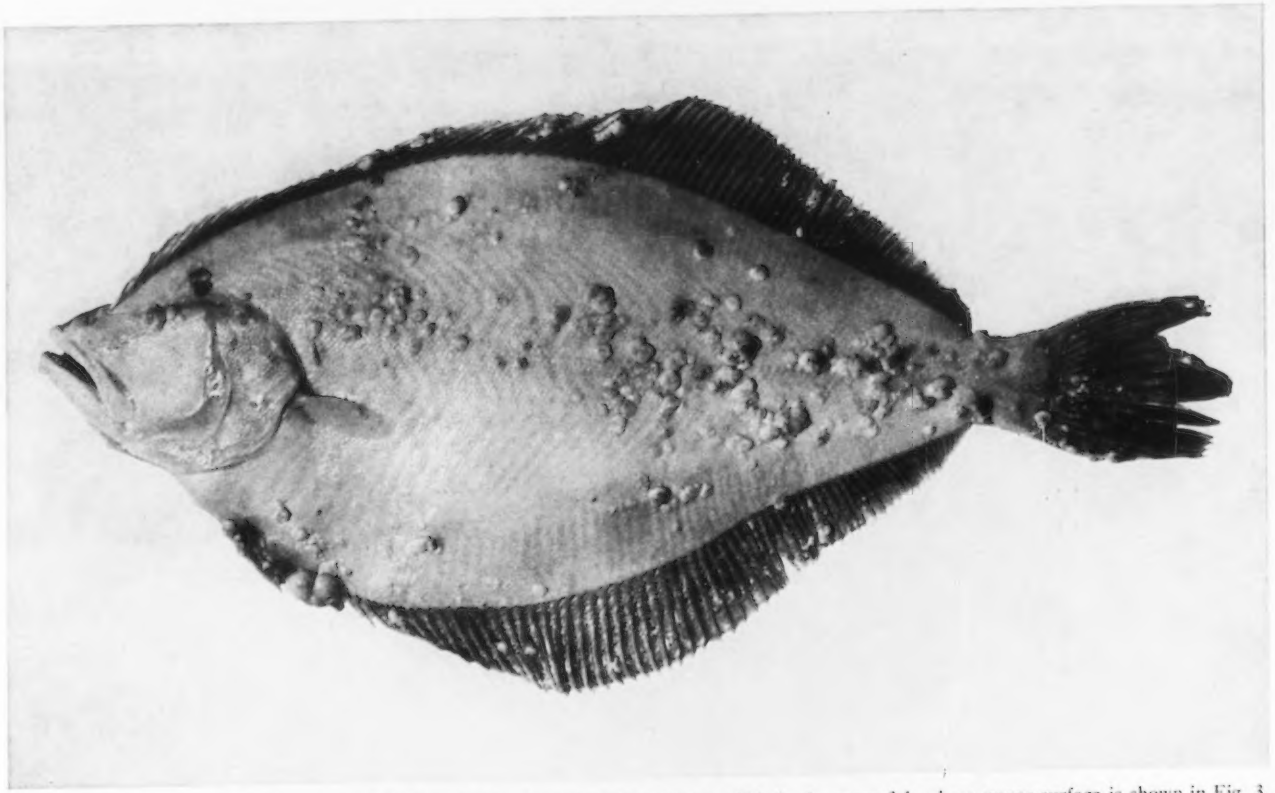

FIG. 4. Lymphocystis infection on the left (lower) side of an American plaice. (This is the same fish whose upper surface is shown in Fig. 3. Shows small tumours composed of lymphocystis cells.)

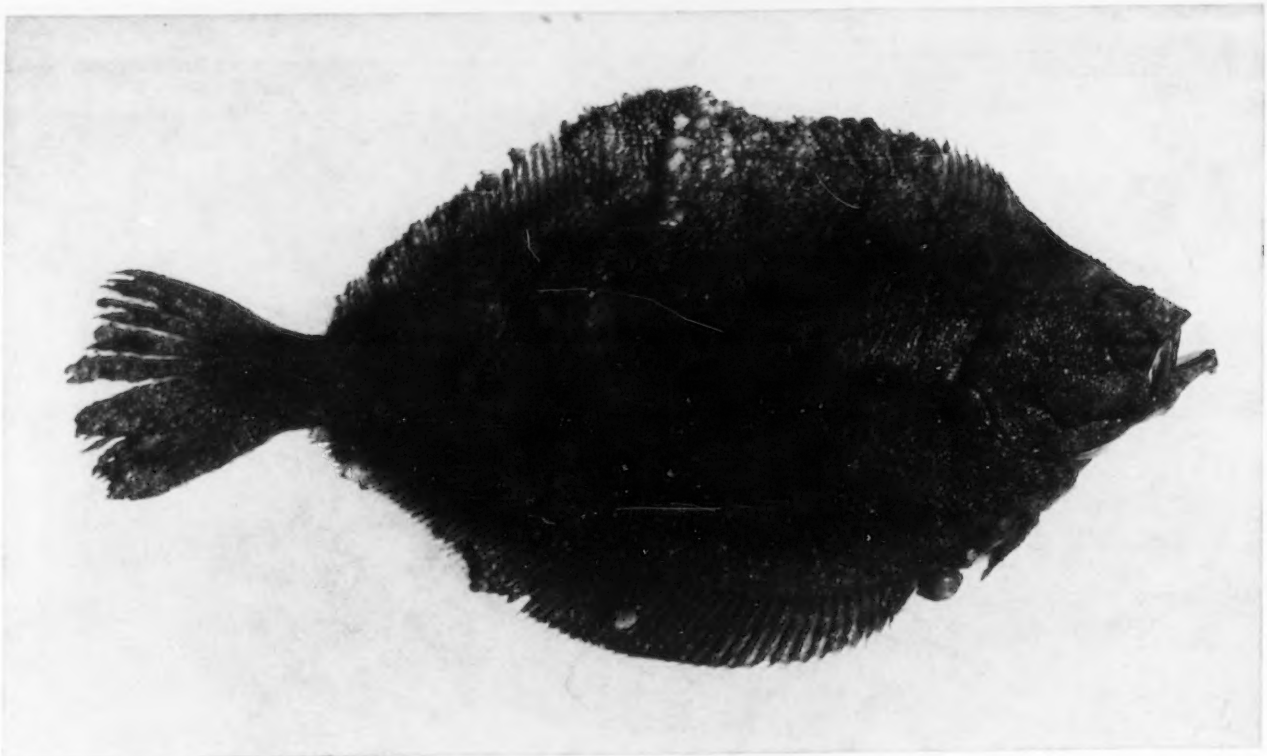

FIG. 5. Lymphocystis infection on the right (upper) side of an American plaice, 43 cm, male mature, testes recovering from spawning. (Ship, date, location, depth as in Fig. 2. Shows large number of individual lymphocystis cells on upper surface, and tumours composed of lymphocystis cells on fins and in front of anal fin.)

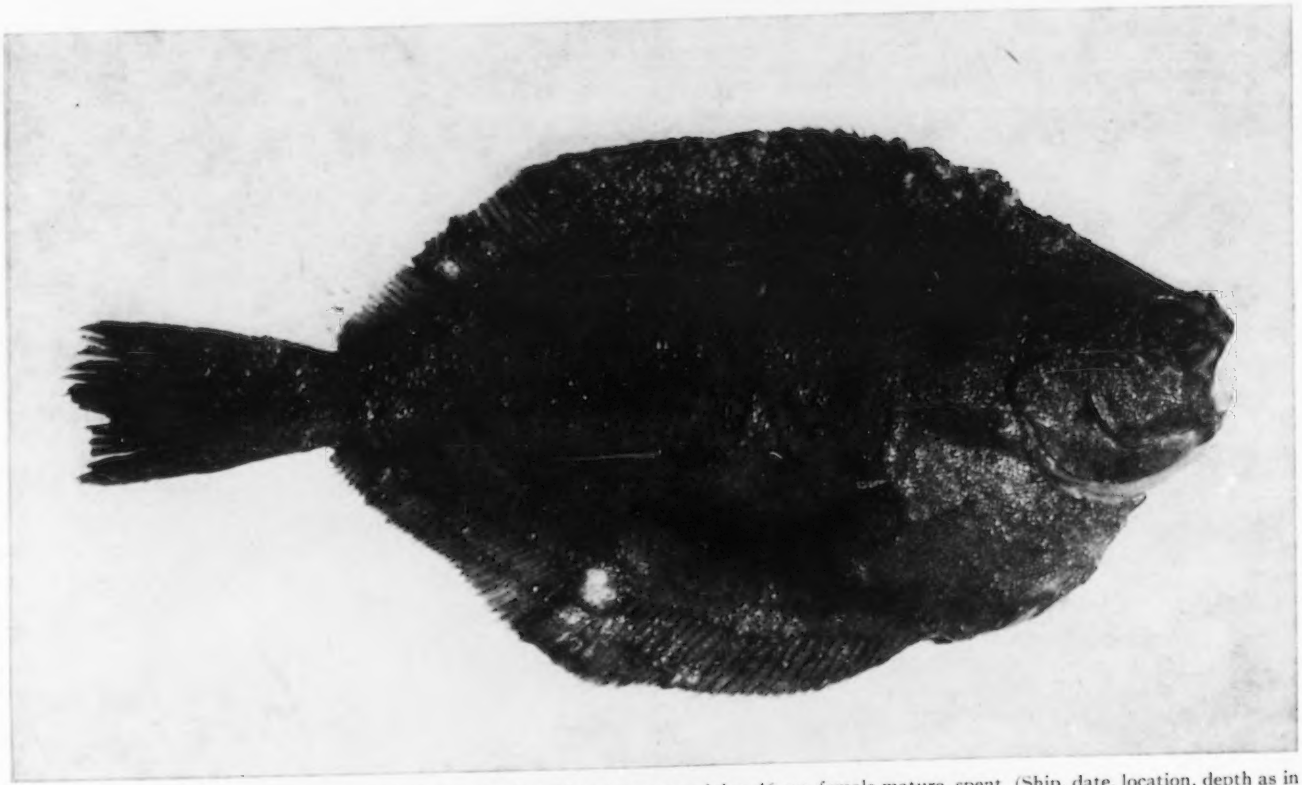

FIG. 6. Lymphocystis infection on the right (upper) surface of an American plaice, 46 cm, female mature, spent. (Ship, date, location, depth as in Fig. 2. Shows individual lymphocystis cells on surface of body, head, and fins, and small and large lymphocystis tumours, in which individual lymphocystis cells may be seen, on dorsal and anal fins.)

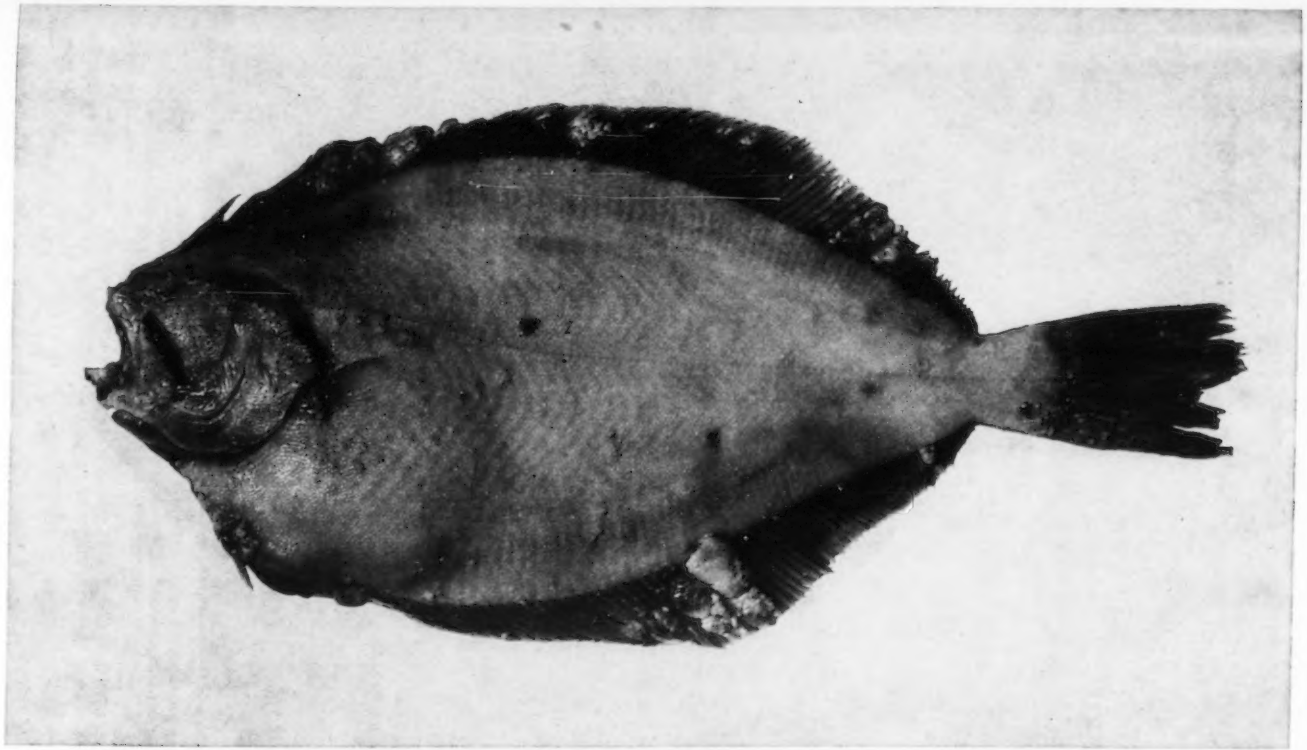

FIG. 7. Identical with Fig. 6, except left (lower) surface. (Shows little infection on body surface, except near fins where there are some individual lymphocystis cells, a few individual lymphocystis cells on caudal, dorsal, and anal fins, and small to large tumours on dorsal and anal fins, around base of ventral fins, and in front of anal fin.)

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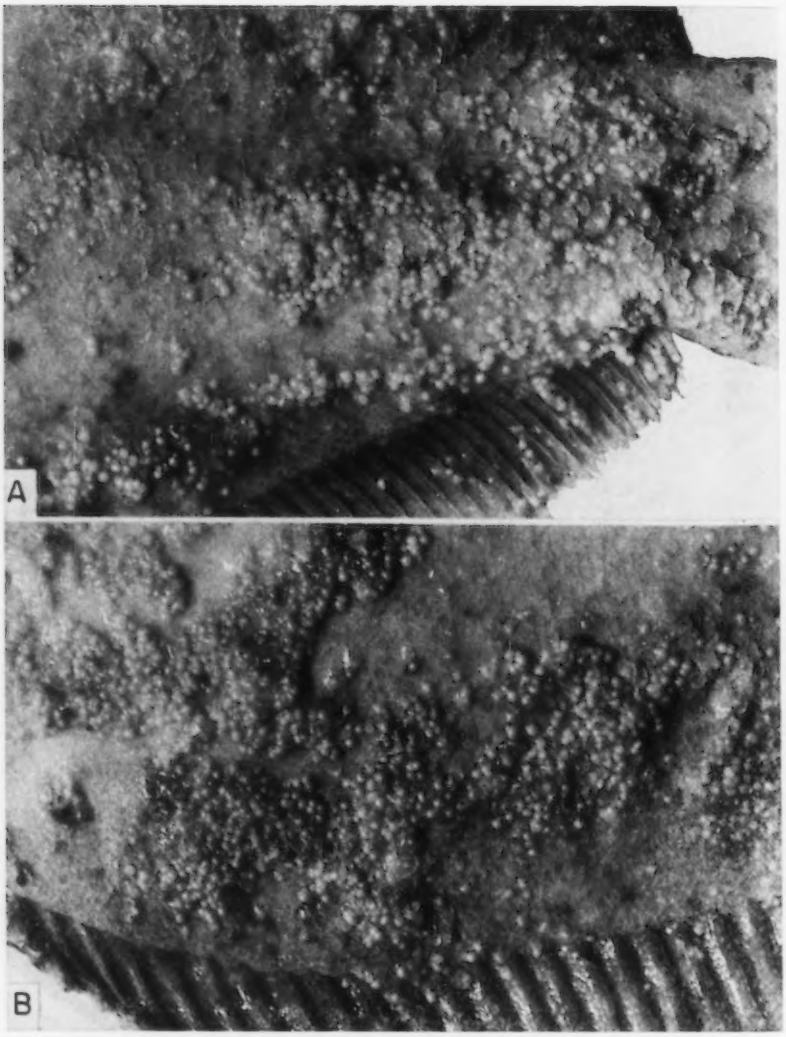

FIG. 8. Lymphocystis cells (natural size) on the posterior part of the left (lower) side of the American plaice of Fig. 1: A, immediately anterior to ventral part of the caudal peduncle; B, immediately above anterior part of anal fin.

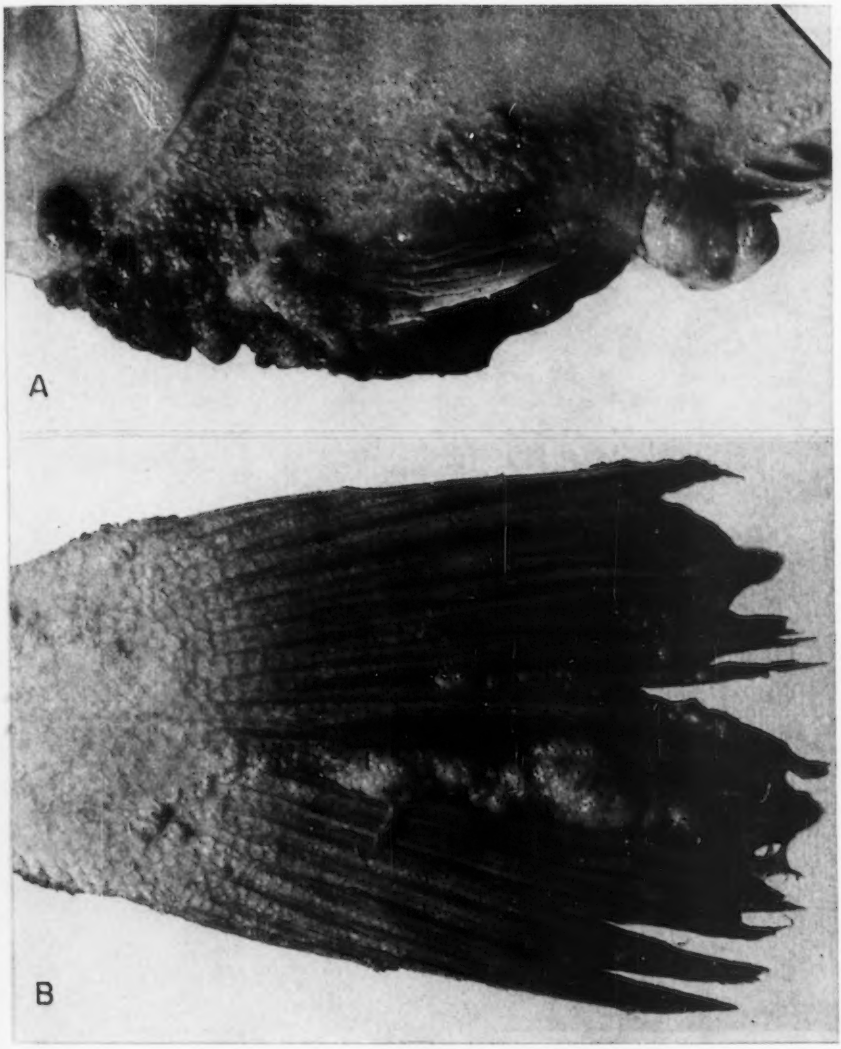

FIG. 9. Lymphocystis cells and larger tumours (natural size) on an American plaice, 54 cm, female mature, new eggs developing, taken by the trawler *Blue Spray*, August 23–29, 1964, on the eastern slope of the Grand Bank between 44°15′N and 45°10′N, at 97–220 m. A, lower surface, conglomeration of individual lymphocystis cells and lymphocystis cells combined as larger tumours between throat and base of ventral fins, large composite lymphocystis tumour in front of anal fin and a few groups of lymphocystis cells on surface of body just above the level of ventral and anal fins; B, smaller and larger composite lymphocystis tumours on lower surface of caudal fin.

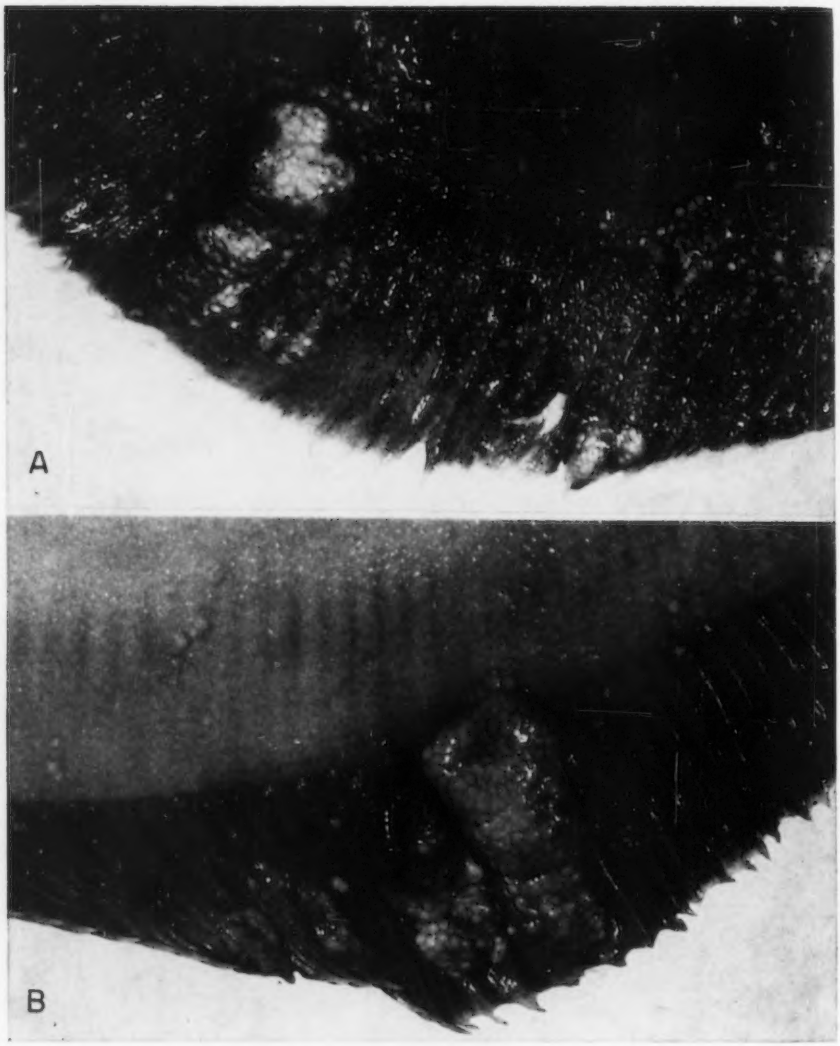

FIG. 10. Composite lymphocystis tumours (natural size) on A, the upper and B, the lower surfaces of the anal fin of the American plaice of Fig. 6 and 7. (The large tumours are parts of the same tumour extending from the upper to the lower sides of the fin. The anterior end is, as in Fig. 6 and 7, to the right in A and to the left in B.)

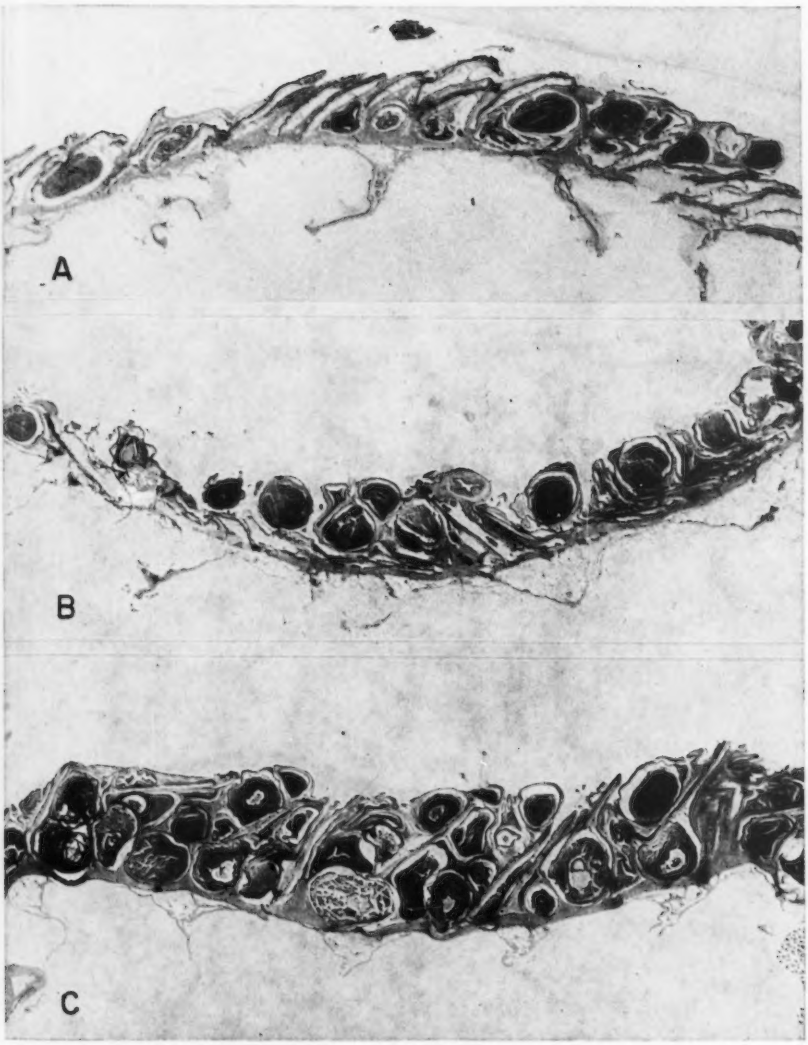

FIG. 11. Sections, × 6.7, through the skin of American plaice showing, A and B, mainly separate lymphocystis cells in the connective tissue of the skin near the upper and lower surfaces of the body, respectively, and C, several layers of lymphocystis cells forming a shallow flat tumour in the skin of the lower surface of the body. (A, from *A. T. Cameron*, September 30–October 12, B and C, from trawler *Blue Spray*, August 1–8. In each case the outer surface faces upward in the figure. Sections are 10 μ and tissues were fixed in 10% formalin after preservation of the fish in ice for at least several days after capture. Staining in these and other sections of Fig. 11–18 was by Ehrlich's acid haematoxylin and eosin. All sections in these figures are from American plaice captured on the eastern Grand Bank in 1964.)

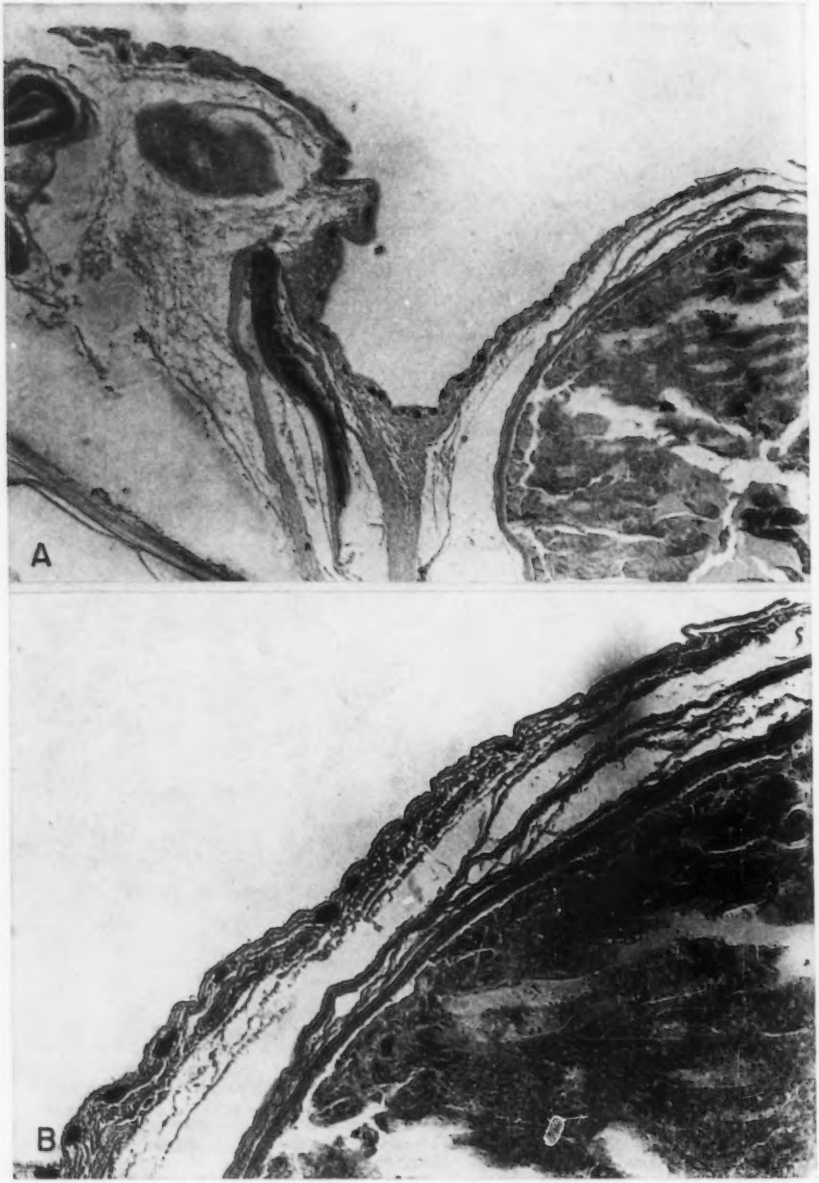

FIG. 12. Partial sections, A × 50 and B × 150, through skin on upper surface of American plaice to show part of the same lymphocystis cell (right), connective tissue and (above and to the left) melanophores below the epidermis. (From *A. T. Cameron*, as in Fig. 11A.)

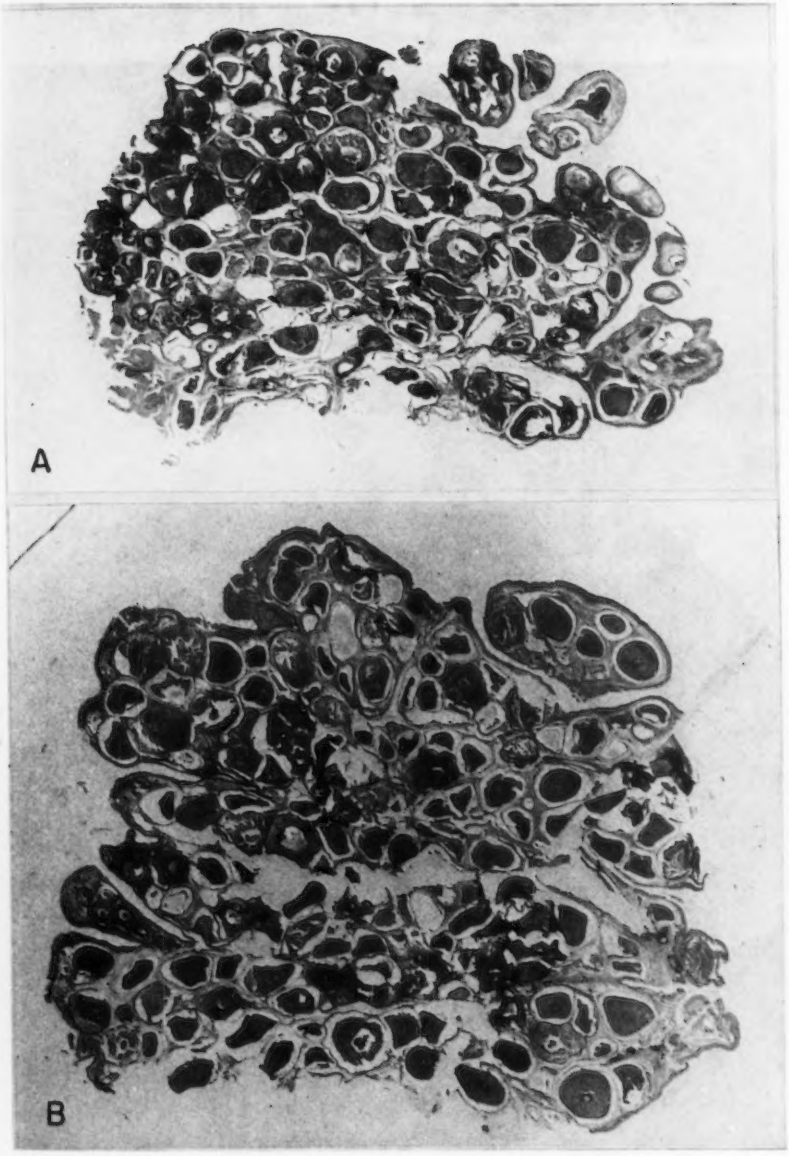

FIG. 13. Sections, × 7.0, through composite external lymphocystis tumours from the skin of American plaice. (Both from trawler *Blue Foam*, November 19–24. Tissues fixed in 10% formalin immediately after capture. Sections are 10 μ (A) and 7 μ (B). In each case the outer part of the tumour, covered with epidermis faces upward and the inner part which has been cut away from the skin faces downward.)

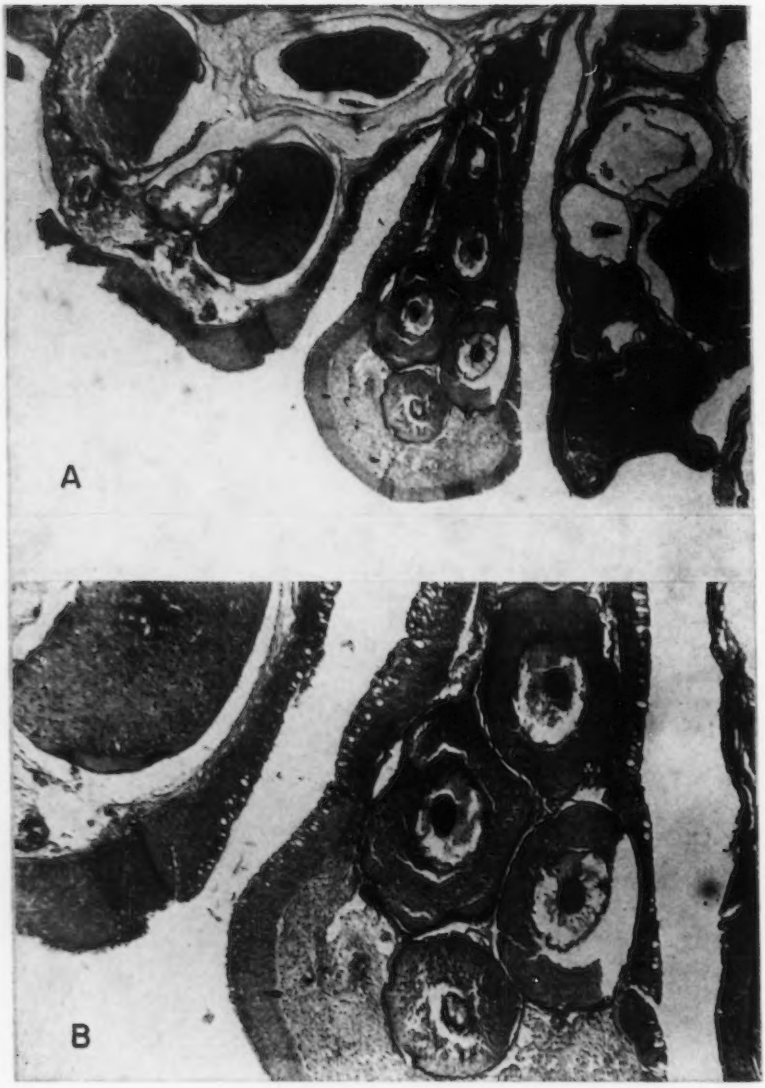

FIG. 14. Section, A × 26, B × 48, of lobes of a composite lymphocystis tumour from the skin of American plaice. (The central lobe with its cells can be seen toward the lower left in Fig. 13B.)

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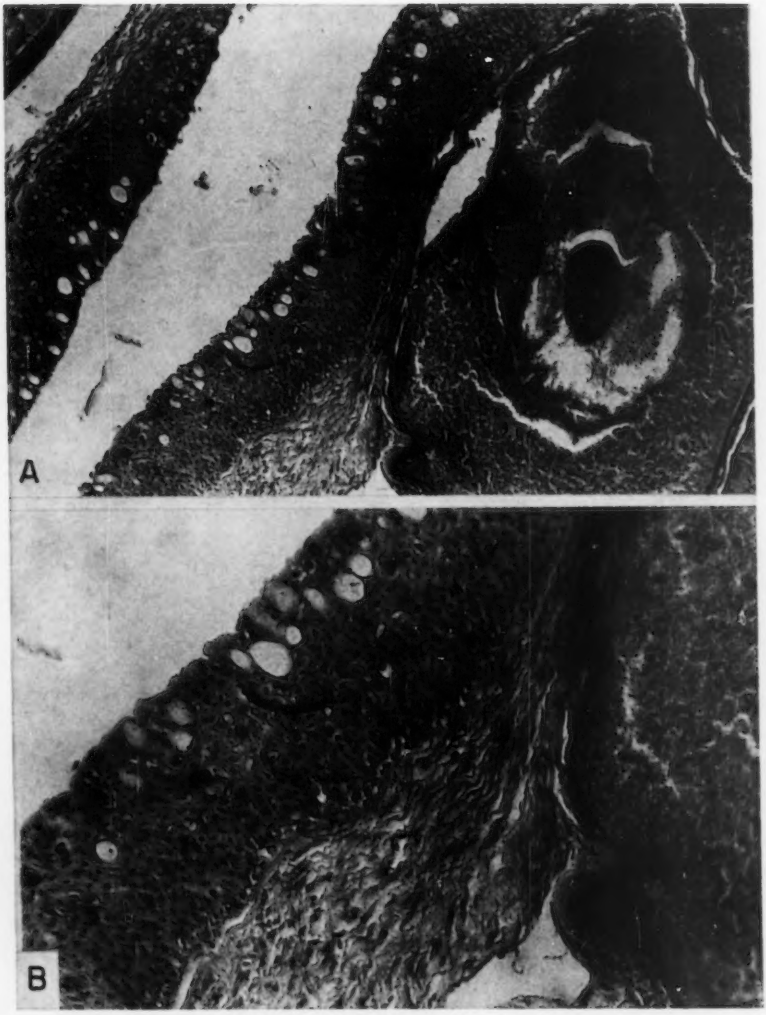

FIG. 15. Section, A × 125, B × 250, through lobes of a composite lymphocystis tumour from the skin of American plaice. (These are higher magnifications of part of a lymphocystis cell and the adjacent connective tissue and epidermis from the lobe shown in Fig. 13B and 14. Part of the epidermis, connective tissue and a tiny section of the cell wall and cytoplasm of a lymphocystis cell from another lobe of the tumour can be seen at the upper left in A.)

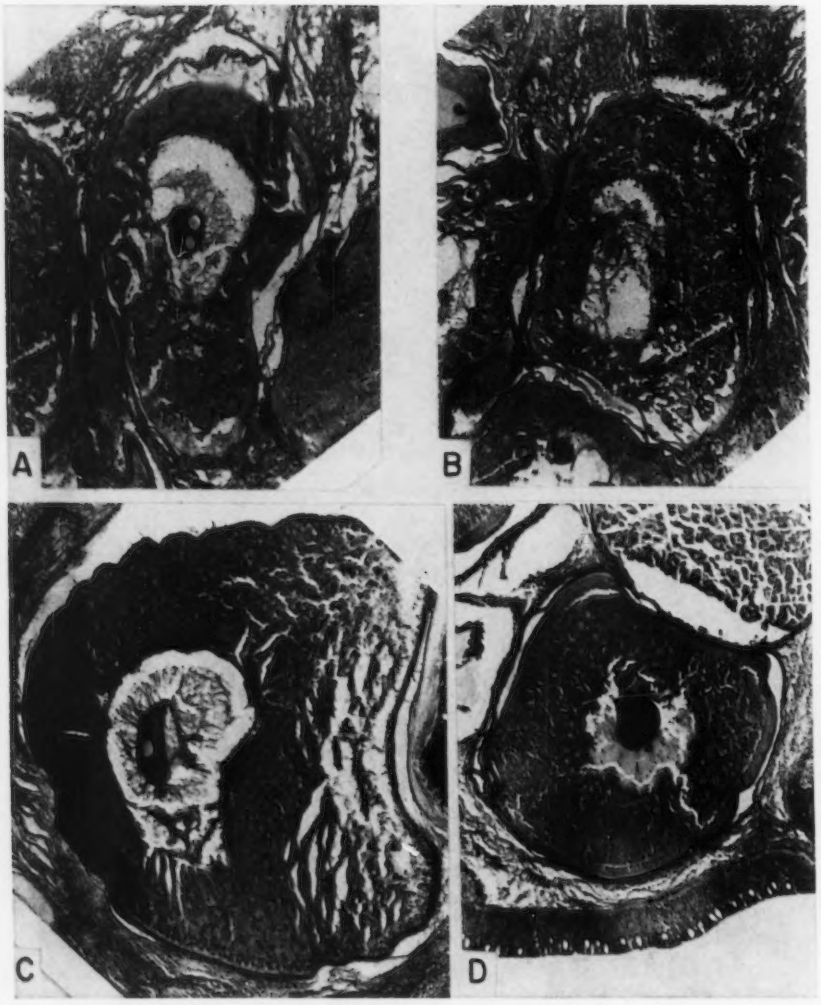

FIG. 16. Lymphocystis cells, × 52, from composite lymphocystis tumours in the skin of American plaice. (From trawler *Blue Spray*, August 1–8, 23–29. Tissues fixed in 10% formalin after at least several days in ice. Cell C can be seen toward the right in Fig. 11C.)

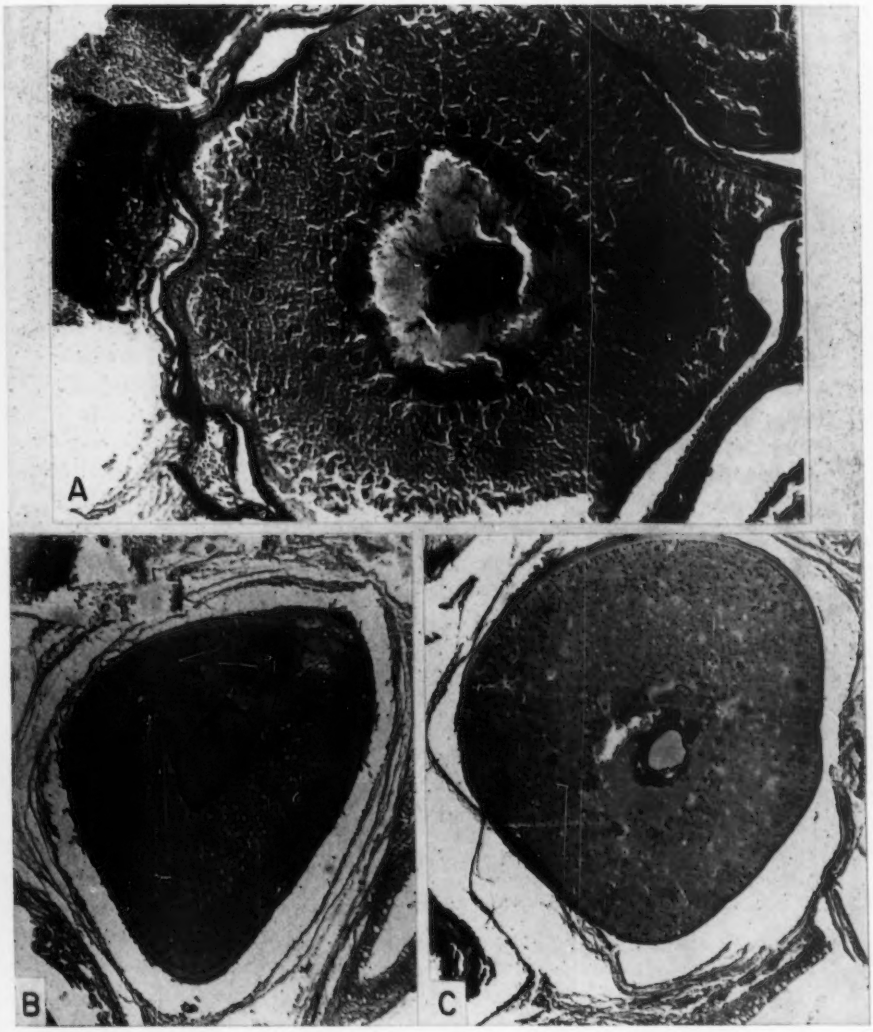

FIG. 17. Sections, A × 138, B × 58, C × 52, of lymphocystis cells from a composite lymphocystis tumour in the skin of American plaice. (From trawler *Blue Foam*, November 19–24. Sections are A, 10 μ and B and C, 7 μ. Tissues fixed in 10% formalin immediately after capture. Cells B and C can be seen in Fig. 13B, lower right.)

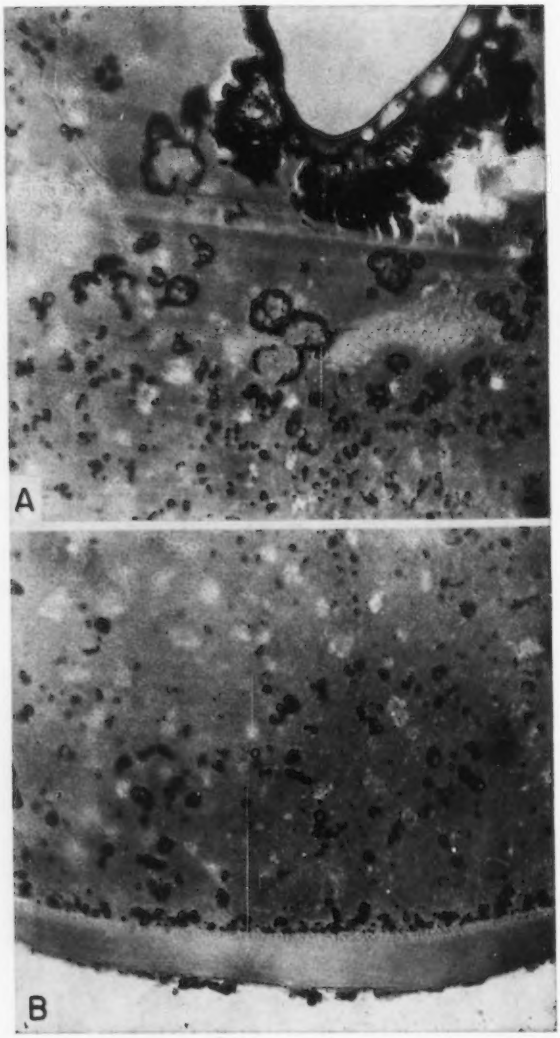

FIG. 18. Higher magnifications, × 250, of parts of the upper right of the lymphocystis cell of Fig. 17C showing cytoplasmic inclusions which according to Weissenberg (1951b) contain granular structures which are the viral particles. (An adjacent section of the same cell, not the same section as in Fig. 17C. The cell wall is below and the nuclear area above.)

It will be noted in many of the figures that the lymphocystis infection of the dorsal and anal fins tends to follow the fin rays rather than the flesh between the fin rays. However, massive infections, resulting in medium to large composite tumour formations, may also occur in the spaces between the fin rays or cover a number of fin rays and spaces.

Microscopic Sections of Individual Lymphocystis Cells and Composite Tumours

Individual lymphocystis cells of the American plaice lie below the epidermis surrounded by the connective tissue of the skin and very near the surface (Fig. 11B, 12) and often between the scale pockets (Fig. 11A). Sometimes there are a number or several layers of lymphocystis cells lying between adjacent scale pockets (Fig. 11C). On the dorsal surface the dark layer of melanophores below the base of the epidermal layer (when normally expanded) (Fig. 12) prevents the pearly whiteness of the lymphocystis cells from being seen as clearly from the upper as from the lower surface where this layer of melanophores is absent. In Fig. 11 and 12 most of the epidermis has apparently been lost owing to the long time between capture and preservation in formalin.

In the composite tumours forming lumps on the skin (Fig. 13–17) the individual lymphocystis cells are surrounded and bound together by connective tissue and the outer part of the lump or of the individual lobes of the lump covered with a thick epidermis. In the outer part of the epidermis are the typical goblet mucous cells (Fig. 14, 15, and 16D).

The giant lymphocystis cells are generally similar in structure to those described for other fishes. Each well-developed cell contains a single large fragile nucleus with a large deeply staining nucleolus (Fig. 14, 15A, 16, 17A). The nucleolus may be vacuolated (Fig. 16A, 16C) and sometimes there may be several smaller nucleoli (Fig. 16A, 17A). Many deeply staining inclusion bodies composed of material which stains like basichromatin are contained within the cytoplasm. These are much more evident in some cells than in others. The typical thick hyaline cell wall is very evident in some lymphocystis cells (Fig. 12, 17, 18B) but the cell wall is not so thick in other lymphocystis cells (Fig. 14, 15, 16A, B).

The lymphocystis cells of American plaice do not fall into a simple pattern with regard to inclusion bodies. There is evidence of inclusion bodies in the form of strings or chains throughout the cell which could be part of a several layered network in both cells of Fig. 16A, B.

There are some cells where the inclusion material is of finer construction appearing as fine dots situated in a ring immediately underneath the cell wall and distributed throughout the cytoplasm with portions of rings or chains situated more centrally (Fig. 17B, C, 18). In some cells in which the nucleus is not apparent there is a dense pattern, presumably of inclusion material, around the nuclear area in addition to the more delicate pattern underneath the cell wall and throughout the cytoplasm (Fig. 17B, C, 18). In these the

fragile nuclear material has apparently disintegrated or disappeared either during the preparation of the sections or earlier. It is possible that the cells of Fig. 17B, C, and 18 are disintegrating, that the cytoplasmic inclusion body network has broken down, and the nuclear and nucleolar chromatin partially disintegrated to form the ring around the nuclear area.

Occurrence and Distribution

American plaice with lymphocystis infection were first reported from the St. John's trawler *Blue Haze*, September 10–18, 1960. Fishing was carried out on the eastern slope of the Grand Bank between 44°00′N–45°10′N and 48°56′W–49°10′W in 80–175 m and 187,000 lb of American plaice were landed from the trip. The crew members said that about 12 infected American plaice were picked out at sea and brought ashore and about 20 others noted at sea were discarded. About 900 lb of American plaice (469 fish) from this catch were examined on both sides at the fish plant but only one infected fish was found. Eight of these American plaice infected with lymphocystis were examined at the Biological Station by the author. Later in the day, in addition to the eight infected fish previously examined, from this trawler's landings 20 American plaice with lymphocystis infection were found by the filleters, brought to the Station, and examined by the author.

Also in the same month, in an otter-trawl survey of the eastern, northeastern, and northern slopes of the Grand Bank by the *A.T. Cameron*, September 9–20, 1960, Mr T. K. Pitt, scientist-in-charge of the cruise, saw several American plaice severely infected with lymphocystis.

In July 1961 an American plaice with a similar lymphocystis infection of the skin was sent to the Station by Fishery Officer D. L. Templeman. This was one of a group taken by a trawler on the eastern slope of the Grand Bank near 46°N and landed at the fish plant at Grand Bank. Mr Templeman reported information from the trawler skippers that quite a number of American plaice from this location were bearing such lumps and nodules, presenting a very unattractive raw material.

A shore examination was also made of random samples of 200–700 American plaice of commercial size landed from five trips of St. John's trawlers between July 16 and October 2, 1964. These American plaice were caught on the southern part of the eastern slope of the Grand Bank between 43°10′N and 45°50′N mainly between 80 and 275 m. Of 1950 American plaice examined, 14 (0.7%) showed nodules or lumps of lymphocystis infection, all in the skin. One was very heavily infected, five heavily, five moderately, and three lightly infected. There was no considerable difference in the severity of the infection during this period (see below), except that fish from the trawler *Blue Haze* had a lower infection rate. This is probably related to a greater discard at sea (see later discussion).

Rate of lymphocystis infection in the skin of American plaice from the eastern slope of the Grand Bank:

Blue Haze,
July 16–22, 1964, 700 plaice examined, 0.3% infected with lymphocystis

Blue Spray,
Aug. 1–8, 1964, 200 " " , 1.0% " " "

Blue Spray,
Aug. 13–18, 1964, 350 " " , 0.9% " " "

Blue Spray,
Aug. 23–29, 1964, 300 " " , 1.0% " " "

Blue Foam,
Sept. 27–Oct. 2, 1964, 400 " " , 1.0% " " "

The skipper and mate of the St. John's trawler *Blue Haze* said (October 1964) that they usually fish the eastern slope of the Grand Bank in the vicinity of 43°30′N, and that south of this position, between 43°N and 43°30′N, the lymphocystis infection becomes much heavier. In handling the American plaice (flounders to the Newfoundland trawler fishermen) on the deck of this ship the method is to pick them up two at a time, and badly infected flounders are thrown over. In places of heavy infection the mate estimated that sometimes 300–400 lb of what they call seedy flounders are thrown away from individual sets. When these heavy infections are encountered the trawlers usually move to other areas where fewer plaice are infected. Between 45°N and 46°N the infection is reported to be less and its occurrence spotty.

The mate on the *Blue Spray*, another St. John's trawler, says that they throw away only half a dozen or so of what they call scabby flounders each trip.

Of the examinations of American plaice landings described above, apart from the July trip of the *Blue Haze* when only two infected fish were found out of 700, about 1% of the fish examined were found to be infected with lymphocystis. Generally between 150,000 and 180,000 lb of these American plaice are caught on a trip. The infection rates in the American plaice from our examinations of commercial landings should be increased to an unknown amount for the *Blue Haze* and very slightly for the other trawlers to allow for discards at sea, but probably the total rate of infection from July to September 1964 was approximately 1%. A closer description of the pattern of the distribution and the actual numbers of infected plaice will require a research vessel survey over the whole American plaice area of the bank.

On a cruise of the *A. T. Cameron* (October 2–11, 1964) to the eastern slope of the Grand Bank between 44°58′N and 45°06′N, American plaice showing lymphocystis infection were noted in some of the sets and were brought to the Station for examination by the author. Of 2027 fish caught at 100 m, at bottom temperatures of −0.56 to 0.23 C, 12 (0.6%) were infected (five males, 32–48 cm; six females, 47–53 cm and one not measured nor sexed). Of 1604 fish caught at 180 m and bottom temperatures of 1.42–1.75 C, 16 (1.0%)

were infected (five males, 34–47 cm; nine females, 47–58 cm, and two not measured nor sexed). Examination at sea was not thorough; mainly the dorsal surface was observed while measuring and some lightly infected individuals may have been missed, but the percentages infected were approximately the same as in the shore examinations.

Possible Explanations of Occurrence of Lymphocystis Disease in American Plaice of the Eastern Grand Bank

In the period 1946–60, previous to the discovery of lymphocystis infection in American plaice, thousands and often tens of thousands of these fish each year were measured and many of them weighed and examined for sex and maturity by the author or other Station scientific and technical staff, and yet the lymphocystis condition was not observed. When the first American plaice found to be infected with lymphocystis in September 1960 were brought to the attention of Mr B. Sears, the fishery inspector at the fish plant at St. John's, he said that he had not previously seen any American plaice infected in this way. The skipper and mate of the St. John's trawler, *Blue Haze*, both of whom had worked as deckhands in the period previous to 1960 and fished for American plaice in the same areas where the disease is now found, said in October 1964 that they had never seen the lymphocystis infection until about 4 years ago.

One is often surprised in biological research by the number of readily apparent occurrences that are not recorded nor even seen because they are not being observed by intelligent or inquiring eyes. However, although before the disease was recognized isolated lymphocystis nodules on the body or fins would probably have been passed without comment by the author and other Station biologists as minor sporozoan infections, it is believed that fish with the great lymphocystis infections seen since 1960 would have been noted by scientists, technicians, fishermen, and fishery inspectors. Apparently the disease has persisted between 1960 and 1964. There are at least four explanations (not necessarily mutually exclusive) of the occurrence of the disease, and it would be difficult to choose between them at present: (1) the infection was present but was not observed; (2) there is a natural periodicity in the intensity of the lymphocystis disease and when it appears it may continue for some time; (3) infection by the lymphocystis virus may be greatly facilitated by injuries to the skin and thus by the intensive otter-trawl fishery for American plaice on the eastern Grand Bank in recent years beginning about 1948 (this fishery may have produced many bruised flounders either by small flounders struggling to get through the meshes of the trawl or by the discarding of bruised live fish from the deck); (4) the virus disease was brought over to the Grand Bank in the nets of European trawlers which had caught infected flounders or plaice in the eastern Atlantic. These infected trawls in the first set or two might infect young American plaice passing out of the net or adult American plaice which are discarded, presumably some of them alive, by the

salt-fish trawlers. However, lymphocystis disease is not recorded from this species (the long rough dab) of the Northeast Atlantic.

The practice of discarding badly infected fish at sea is not a good one, since apparently the virus can live a long time in the water or bottom sand after the lymphocystis cells decay. The infected fish should be brought in and put through the meal plant. The numbers presently discarded, however, may have a negligible effect in relation to the total sources of lymphocystis infection.

The viral infection leading to lymphocystis disease is a disease of fishes and not of humans.

ACKNOWLEDGMENTS

I am grateful to Dr Z. Kabata for his identification of the lymphocystis type of infection and to Messrs T. K. Pitt, D. L. Templeman, L. N. Cluett, and others who supplied information on the infected plaice, also to Mr A. T. Pinhorn and Miss Alma M. Holland who prepared the slides of the tissue sections, and to Dr Ross F. Nigrelli and Mr V. M. Hodder who read the paper and offered suggestions for improvement. Photographs are by Mr E. L. Rowe.

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The Food of the Pike, *Esox lucius*, in Heming Lake, Manitoba[1]

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ABSTRACT

The stomach contents of 29,477 northern pike (*Esox lucius*) captured mainly in gill nets at Heming Lake, Manitoba, between 1950 and 1962 were examined. The food consisted almost exclusively of fish: trout-perch (*Percopsis omiscomaycus*) and yellow perch (*Perca flavescens*). Other fish included common suckers (*Catostomus commersoni*), spottail shiners (*Notropis hudsonius*), sticklebacks (*Eucalia inconstans* and *Pungitius pungitius*), pike, burbot (*Lota lota*), whitefish (*Coregonus clupeaformis*), tullibee (*Leucichthys* sp.), yellow walleye (*Stizostedion vitreum*), cottid (*Cottus cognatus*), and darters (*Etheostoma nigrum*). Among invertebrates were crayfish, mayflies, dragonflies, caddisflies, and leeches. Ducks, small mammals, and frogs formed an insignificant part of the diet. Seasonal variation in food content and annual variation in the degree of feeding were evident. Trout-perch were important as food items in May and June, the spottail shiner in July, the yellow perch in August and September, and stickleback between October and March. Coregonine fishes, important in the life-cycle of *Triaenophorus crassus* but of minor importance as pike food, occurred in higher concentrations in October. There appeared to be annual differences in the degree of feeding, possibly related to differences in temperature. The frequency of empty stomachs from pike caught by angling and in gill nets was approximately the same. No obvious differences were noted in feeding habits of male and female pike, but there were some minor differences in the food of pike from shallow and deeper water habitats. Over an 11-year period of intensive fishing, there did not appear to be any unusual changes in the food habits of pike. The size of the prey is related to the size of the pike. There is a marked increase in the number of small perch, trout-perch, and spottail shiners consumed by pike of increasing size. The possible effects of the predator (pike) on other prey species is discussed. Relative abundance and seasonal availability appeared to determine the incidence of prey consumed. The reduction in the average size of the pike appears to have had some effect on the survival of other species of fish.

INTRODUCTION

The pike (*Esox lucius*) harbors the adult cestode, *Triaenophorus crassus*, whose life history has been under investigation at Heming Lake, Manitoba, since 1945. The pike population has been exploited in the hope of reducing and/or eliminating the parasite which, in its resting stage in the flesh of the commercially important whitefish (*Coregonus clupeaformis*), affects the marketability of this species. The pike were examined primarily to determine the quantities of whitefish and ciscoes (*Leucichthys* sp.) eaten by pike in order to understand what level of consumption of coregonines is necessary to propagate the life-cycle of the tapeworm. As the pike also harbors the adult cestode, *T. nodulosus*, for which several species of fish act as intermediate hosts, it was necessary to at least make some qualitative analysis of pike stomach contents which would provide information of a general nature on the food and feeding habits of pike.

[1]Received for publication February 24, 1965.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

It would also demonstrate the relationship of these to other fish in the lake, and assist in understanding the complexities of the cestode interrelationships. The present paper is based on an examination of the stomach contents of 29,477 fish from 3.5 to 100 cm (1.4–39.5 inches) long caught from 1950 to 1962. Most of the fish were captured between May and October, but some samples were taken in winter months.

MATERIALS AND METHODS

The pike stomachs examined in this study were from pike captured by hoop nets, trammel nets, trap nets, seines, gill nets, and by the use of emulsifiable rotenone. Rotenone was used to capture, for growth studies, pike too small to be taken by the other methods of capture. It was soon learned, however, that fish taken by this method could not be used in food studies, as those fish which succumbed early were preyed on by the more resistant fish with the result that the more resistant fish had gorged stomachs when they finally died from the effects of the poison. The majority of pike examined were captured with gill nets of various mesh sizes ranging from 3.7 to 13.3 cm ($1\frac{1}{2}$–$5\frac{1}{4}$ inches) stretched measure which, in most cases, were lifted once every 24 hr. The gill nets were usually lifted early in the morning and, as movement studies[2] have shown that the pike are most active during the night and early in the day, little digestion probably occurs between the time of capture and examination. The pike does not appear to regurgitate its stomach contents as readily as the yellow walleye (*Stizostedion vitreum*) when enmeshed.

The food organisms were individually counted and identified, in most cases to species, but where digestion had proceeded to the point where the food was only recognizable as fish remains, they are referred to as unidentified fish or fish remains, with the exception of very small forage fish. Most of the fish in the stomachs were measured.

The stomach contents were recorded as the number of pike containing each food item (frequency of occurrence) and the number of each organism present in the stomach. The percentage figures for frequency of occurrence and the figures of average number of organisms consumed are based on the total number of pike examined, not only on those which contained food. As this was the method used by Frost (1954) in a comprehensive description of the food of pike of Lake Windermere, it was possible to compare results from two widely separated regions.

General Description of the Food of Pike

The type and quantity of food eaten by pike covering the period 1950–62 inclusive is given in Table I. The frequency of occurrence (percentage) and the average number of each organism per pike affords some indication of the relative

[2]Details are available in a mimeographed manuscript report (No. 542) which is available at all establishments of the Fisheries Research Board of Canada.

importance of each food type. Consideration of the possible influence of seasonal variation on the annual food will be discussed later.

The diet is almost exclusively one of fish, and in the last column (Table I) trout-perch (*Percopsis omiscomaycus*), unidentified fish and perch (*Perca flavescens*) are seen to be the main species eaten. White suckers (*Catostomus commersoni*), spottail shiners (*Notropis hudsonius*), and sticklebacks (*Pungitius pungitius* and *Eucalia inconstans*) are also large contributors to the diet of the pike. The pike, burbot (*Lota lota*), coregonine fish, yellow walleye, cottid (*Cottus cognatus*), and darter (*Etheostoma nigrum*) contribute almost negligible amounts. Other vertebrates, including ducks, small mammals (mice, shrews, and muskrats), and frogs form an insignificant fraction of the diet. Among the invertebrates consumed are crayfish, mayflies, dragonflies, caddisflies, and leeches, but the combined invertebrate foods only occurred in 4.4% of all pike examined over the period of the investigation.

There are minor annual variations in the main types of food eaten and some species are predominant in one year and of lesser significance in other years. For example, in the years 1950–53 the trout-perch was the most frequently occurring food item, but in 1954 it was supplanted by perch and even spottail shiners. To establish the relative importance of each of the major food items, the data from Table I were further analyzed by years and ranked (Table II) according to their frequency of occurrence and average number of organisms present over the 13-year period. These results show the predominance of fish in the diet of pike and accentuate the importance of trout-perch as a food. The relative unimportance of coregonines in the diet is evident. Frost (1954) and Allen (1939) found the perch (*Perca fluviatilis*) predominant over all other fish in the diet of Lake Windermere pike.

Food of Small Pike

Few stomachs of very young pike were examined, as most of these fish were taken by poisoning. It has been previously shown that fish taken by these methods are not suitable for food studies.

Some stomach analyses were made of the occasional small pike taken by seining in 1959 and of small pike that appeared in the gill net catches. A special sample was taken by seine in late August of 1963 to complement the more extensive food study on larger fish.

The smallest fish (3.5 cm long) contained *Epischura*, *Bosmina*, and an unidentified fish. The next smallest (4 cm) contained unidentified fry remains and a trace of *Epischura*. Another pike (8.5 cm) had *Hyalella* and fish. Above this size, no zooplankters or bottom organisms were found and the diet was mainly suckers, darters, trout-perch, spottail shiners, and unidentified fish.

SEASONAL FOOD OF PIKE

The food of pike for different months of the year for the combined years 1950–62 is shown in Fig. 1. The data in Fig. 1 represent the number of pike containing each food expressed as a percentage of the total number of pike

TABLE I. The frequency of occurrence (%) and the average number of each organism (shown in parentheses) consumed by pike during the years 1950–62 at Heming Lake.

	Year													Average
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1950–62
Pike (*E. lucius*)	2.5 (0.02)	2.9 ...	1.0 (0.01)	1.2 (0.01)	1.3 (0.01)	1.7 (0.02)	1.5 (0.016)	1.4 (0.014)	0.3 (0.003)	0.6 (0.006)	0.1 (0.001)	...	0.44 (0.006)	0.81 (0.008)
Whitefish (*C. clupeaformis*)	0.4 (0.003)	0.45 ...	0.4 (0.004)	0.36 (0.003)	0.48 (0.004)	0.42 (0.004)	0.37 (0.004)	0.6 (0.006)	0.04 (0.004)	...	0.01 (0.0001)	...	...	0.21 (0.002)
Cisco (*Leucichthys* sp.)	...	0.23 ...	0.32 (0.003)	...	0.38 (0.003)	...	0.16 (0.002)	0.02 (0.0002)	0.04 (0.0004)	...	...	...	...	0.06 (0.0005)
Walleye (*S. v. vitreum*)	...	...	...	0.07 (0.0007)	0.57 (0.005)	0.15 (0.0015)	0.04 (0.0004)	0.24 (0.002)	0.04 (0.0004)	...	...	...	...	0.08 (0.0008)
White sucker (*C. commersoni*)	6.8 (0.09)	6.8 ...	5.5 (0.06)	6.3 (0.069)	7.4 (0.10)	6.2 (0.07)	5.5 (0.08)	4.1 (0.04)	6.2 (0.069)	9.1 (0.09)	2.6 (0.02)	30.4 (0.32)	8.1 (0.11)	5.3 (0.06)
Yellow perch (*P. flavescens*)	8.1 (0.32)	8.9 ...	2.8 (0.04)	6.2 (0.10)	11.2 (0.16)	6.6 (0.15)	12.2 (0.27)	23.6 (1.15)	5.2 (0.061)	10.5 (0.21)	6.6 (0.14)	10.8 (0.13)	10.6 (0.38)	9.2 (0.26)
Burbot (*Lota lota*)	1.5 (0.015)	0.23 ...	0.24 (0.002)	1.1 (0.01)	0.7 (0.008)	0.05 (0.006)	0.7 (0.007)	0.08 (0.008)	0.02 (0.002)	0.4 (0.004)	...	...	...	0.41 (0.004)
Unid coregonine	...	1.1 ...	0.08 (0.0008)	0.29 (0.002)	0.48 (0.004)	0.15 (0.0015)	0.08 (0.0008)	0.05 (0.0005)	0.08 (0.0008)	...	...	...	...	0.09 (0.0008)
Unid fish	9.5 (0.14)	5.9 ...	12.9 (0.14)	7.2 (0.11)	6.6 (0.11)	10.2 (0.11)	9.4 (0.11)	8.3 (0.11)	11.0 (0.13)	12.1 (0.15)	12.6 (0.17)	13.0 (0.15)	14.5 (0.24)	10.6 (0.13)
Trout-perch (*P. omiscomaycus*)	40.1 (3.5)	36.3 ...	21.0 (1.25)	9.4 (0.53)	5.3 (0.22)	8.8 (0.41)	7.5 (0.33)	13.5 (0.54)	11.8 (0.23)	15.0 (0.36)	15.0 (0.19)	2.2 (0.08)	14.3 (0.38)	14.1 (0.40)
Sticklebacks (*Eucalia inconstans, Pungitius pungitius*)	...	0.9 ...	3.4 (0.93)	9.0 (0.53)	12.1 (0.59)	3.5 (0.09)	0.8 (0.01)	0.5 (0.03)	7.1 (0.15)	5.8 (0.16)	2.8 (0.04)	0.9 (0.17)	2.8 (0.05)	4.2 (0.15)
Spottail shiner (*N. hudsonius*)	10.3 (1.2)	5.2 ...	3.9 (0.07)	3.8 (0.15)	2.9 (0.06)	3.4 (0.12)	6.0 (0.26)	5.8 (0.18)	7.0 (0.08)	5.8 (0.13)	15.6 (0.22)	4.3 (0.04)	3.8 (0.11)	8.1 (0.17)
Mayflies	0.4 (0.05)	...	...	0.94 (0.01)	2.7 (0.027)	3.2 (0.04)	0.03 (0.04)	0.5 (0.10)	0.45 (0.09)	1.8 (0.02)	0.05 (0.008)	0.2 (0.02)	2.0 (0.04)	2.6 (0.04)

Miscellaneous larvae	...	...	...	...	...	0.42 (0.005)	0.05 (0.005)	0.1 (0.001)	0.04 (0.0004)	0.04 (0.005)	...	...	...	0.09 (0.001)
Cottus sp.	.04 (0.01)	0.45 ...	0.16 (0.001)	0.14 (0.001)	0.19 (0.001)	0.26 (0.002)	...	...	0.14 (0.002)	0.5 (0.005)	0.016 (0.002)	...	...	0.16 (0.002)
Darter (*E. nigrum*)	...	...	0.08 (0.0008)	0.14 (0.001)	0.38 (0.005)	0.05 (0.0005)	0.08 (0.0008)	0.08 (0.0008)	0.17 (0.002)	0.03 (0.003)	...	...	...	0.11 (0.001)
Aquatic insects	0.2 (0.002)	0.7 ...	5.4 (0.06)	1.4 (0.014)	2.9 (0.029)	0.5 (0.005)	0.8 (0.08)	0.2 (0.002)	0.14 (0.001)	...	0.01 (0.0003)	...	...	0.58 (0.006)
Dragonflies	...	...	...	...	...	0.2 (0.002)	0.02 (0.003)	0.05 (0.007)	0.09 (0.0009)	0.1 (0.001)	0.01 (0.0008)	...	...	0.13 (0.001)
Crayfish	1.3 (0.02)	2.0 ...	1.8 (0.02)	1.0 (0.01)	1.2 (0.012)	0.13 (0.01)	1.7 (0.03)	0.6 (0.007)	0.09 (0.0009)	...	0.04 (0.0004)	...	0.22 (0.002)	0.56 (0.007)
Caddis fly	...	...	...	...	...	0.10 (0.0015)	...	...	0.07 (0.0008)	...	...	...	...	0.02
Leeches	...	...	...	0.29 (0.002)	0.19 (0.001)	0.42 (0.008)	0.16 (0.0016)	0.1 (0.001)	0.5 (0.006)	0.08 (0.0008)	0.05 (0.0007)	...	...	0.22 (0.003)
Vegetation	...	...	...	...	...	0.05 (0.0005)	0.12 (0.001)	0.3 (0.003)	0.07 (0.0007)	0.08 (0.0008)	0.11 (0.0001)	...	...	0.07 (0.0008)
Duck remains	...	...	...	...	...	0.05 (0.0005)	...	...	...	...	...	...	...	0.003 (0.00003)
Mammals	...	...	...	0.2 (0.002)	...	0.05 (0.0005)	0.12 (0.001)	0.19 (0.0019)	...	...	...	...	...	0.04 (0.0005)
Ligula	...	...	...	...	...	...	...	0.16 (0.0019)	0.05 (0.0005)	...	0.11 (0.001)	...	0.6 (0.006)	0.07 (0.0008)
Frog remains	...	0.23 ...	...	0.2 (0.002)	...	...	...	...	...	...	...	...	...	0.01 (0.0001)
No. of pike examined	516	438	1240	1374	1048	1880	2393	3636	7018	2300	7134	46	454	29,477
Percentage empty	33.1	31.5	48.5	58.3	48.2	57.4	54.9	37.6	46.8	46.9	48.3	34.7	50.4	45.5
Percentage feeding	67.0	68.5	51.5	41.7	51.8	42.6	45.1	62.4	53.2	53.1	51.7	65.3	49.6	54.5

TABLE II. Relative ranking importance of major food items in 29,477 pike stomachs examined during the years 1950–62.

Rank	Frequency of occurrence (%)	Average No. of organisms per stomach
1	Trout-perch	Trout-perch
2	Unidentified fish	Perch
3	Perch	Unidentified fish
4	Sucker	Sticklebacks
5	Spottail shiner	Spottail shiner
6	Stickleback	Sucker
7	Pike	Mayfly
8	Mayfly	Pike
9	Aquatic insects	Crustaceans
10	Whitefish Burbot	Burbot
11	Unidentified coregonine	Whitefish
12	Cisco	Unidentified coregonine Cisco

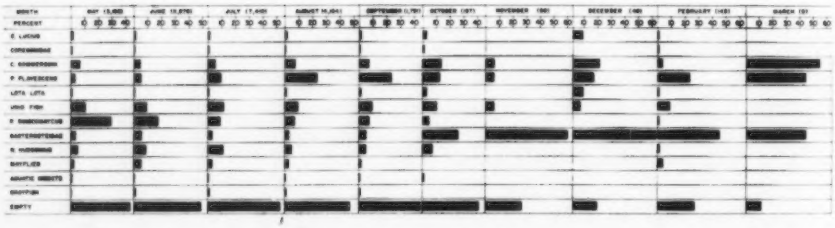


FIG. 1. The number of pike containing each type of food expressed as a percentage of the total number of pike stomachs examined each month for the combined years 1950–62.

stomachs examined for each month. The data are rather meagre for the winter months, but are sufficient to indicate the relative types of food consumed. Unidentified fish were usually fry or fingerling size so completely digested as to be unrecognizable. These unidentifiable remains were found in 6–10% of all pike stomachs examined in most months.

Very definite seasonal changes in the food of pike are noticeable in the data. In May 20% and in June 17.5% of all pike stomachs contained trout-perch. The percentage frequency occurrence decreases with each succeeding month and no trout-perch were found in November, December, or March.

Less than 1% was recorded from stomachs examined in February. The high incidence of trout-perch as food in May and June probably results from the spawning of the trout-perch inshore and upstream in early May.

The yellow perch is the second most important of all the foods eaten. There is a gradual increase in the occurrence of perch through May, June, and July, and in August and September it is found in over 20% of the stomachs. Perch occur in less than 15% of the pike stomachs in October and November, but become more frequent in December, February, and March. It would appear that the perch move from deeper water in August and September when the water temperature is rapidly becoming cooler and thus are more available to the pike.

In July the spottail shiner occurred in slightly more than 10% of the pike examined, but even this percentage frequency was greater than any of the other species usually found. Spottail shiners were found in lesser quantities in the other spring and summer months, but were rarely observed in the cold weather months.

The white sucker occurred in less than 10% of the stomachs examined between May and September, but was of apparent greater importance in December and March. However, in these months the samples were probably too small to be of much significance. The low frequency of occurrence of suckers in the diet of pike is difficult to explain, particularly as there was a marked increase in the number of small suckers in the lake during the latter years of the study.

Members of the family Gasterosteidae (*Eucalia inconstans* and *Pungitius pungitius*) are found in pike stomachs in all months under investigation, but occur infrequently (<5%) between May and September. In October over 25% of the stomachs contained sticklebacks, and in the winter months from November to March they are present in even greater numbers. In the fall months the pike stomachs were frequently described as being "gorged," often containing 75–100 sticklebacks. The sticklebacks spawn in shallow water, but leave in early spring for the deeper waters of the lake where they are not in close association with the pike; however, with the approach of freeze-up they move back to the shallow water.

Between May and September pike appeared in 1% of the pike stomachs, but in October there was a marked increase in the number eaten, and in the small December sample the frequency of occurrence was 7%. Members of the family Coregonidae prefer deep cool water, but are inshore for spawning in October and again about the time the ice leaves the lake in the spring. Although their incidence in pike stomachs is extremely low, there was a minor increase in their frequency in October when they would be more closely associated with the pike. The burbot was more frequently found in pike stomachs in late fall and winter than in the summer.

Mayfly nymphs and larvae and crayfish were the most important of the invertebrates found. Mayflies were found in approximately the same frequency of occurrence in summer and winter. Crayfish were of approximately the same

frequency of occurrence from June to September, but none was found during the fall and winter.

In summary, the most important food types eaten in each of several periods during the year are as follows: May and June — trout-perch; July — spottail shiner; August to September — perch; October to March — sticklebacks.

Martin (1957) noted differences in the frequency of forage fish in lake trout (*Cristivomer namaycush*) diet as the absence of thermal barriers permitted the lake trout to feed on species unavailable during thermal stratification. There were twice as many perch as whitefish in the winter and just the reverse in the summer.

In general agreement with the findings of Frost (1954), the seasonal changes in the diet of the pike of Heming Lake appear to be related to the availability of the fish food species, which, as she describes, is "an expression of the seasonal changes in habit of the different fishes." The different species composition of the two lakes permits only very general comparisons. Perch are important food species in both lakes and at approximately the same time; however, in May and June in Heming Lake the trout-perch appears to fill the prey role occupied by the perch in Lake Windermere. Whereas sticklebacks are eaten mainly in May and June in Windermere and are of little importance, in Heming Lake they are of major importance in the winter months. The pattern of cannibalism is about the same in both lakes. The char and brown trout of Windermere are eaten mainly during the winter months, and although the coregonines of Heming Lake are not prominent items in the diet, there is some indication that more are consumed in winter than in summer.

CHANGE IN FOOD HABITS DURING EXPLOITATION OF PIKE POPULATION

Because of the change in size of the pike during the exploitation period 1950–60,[3] it was thought that there might also have been a change in the diet. The percentage frequency of occurrence of the major items in the pike diet for each month in each year is shown in Fig. 2. The frequency of occurrence of trout-perch in May declined during the investigation, but for the remaining summer months there were minor fluctuations followed by a gradual increase during the years 1958, 1959, and 1960. One explanation for the change in May is that during the early 1950s a large percentage of the pike catch was from hoop nets set in creek mouths and from angling carried out near creek mouths, thus the pike that were sampled had been in very close association with the trout-perch returning to the lake from spawning. In the latter years the pike were more numerous, fishing was more intensive, and possibly the trout-perch population was also at a fairly high level.

During the investigation the perch population underwent drastic changes, possibly as a result of the change in the predator population, and these changes

[3]Data are on file at the Fisheries Research Board of Canada, Biological Station, 539 Richmond Street, London, Ontario.

were reflected in their contribution to the pike's diet. It would appear that pike were eating more perch in the 1956–60 period than in the previous 5 years of the study. In years of high perch abundance, i.e. 1957 and 1959, there was a corresponding high incidence of perch in pike stomachs. The decrease in the contribution of perch to the diet in 1958 is most striking, especially as small perch were abundant in the lake. Lawler (1963) also noted a decrease in the incidence of perch in burbot stomachs in 1958.

There did not appear to be any trend towards higher predation on sticklebacks with time, and only minor annual fluctuations in the incidence of sticklebacks in the stomachs were evident. It is interesting to note that there were peaks in incidence of sticklebacks in each month of 1954 and 1958.

During the period of heavy fishing for pike, other fish were inadvertently exploited and among those which showed the most dramatic change was the white sucker. The average size of the suckers decreased, but the number captured reached unusually high proportions, the ultimate catch being 17,000 suckers in 1960. It is interesting to observe that there was only a minor increase in the consumption of suckers by pike in those years of high sucker density. The years 1954 and 1958 were peak years of incidence of occurrence for suckers as they were for the sticklebacks.

There were years in which the frequency of occurrence of spottail shiners was considerably higher than others, and there is some indication of a trend to slightly higher frequency of occurrence in latter years, particularly during June, July, and August. Peaks of incidence of occurrence were fairly consistent for most months in 1956 and 1960.

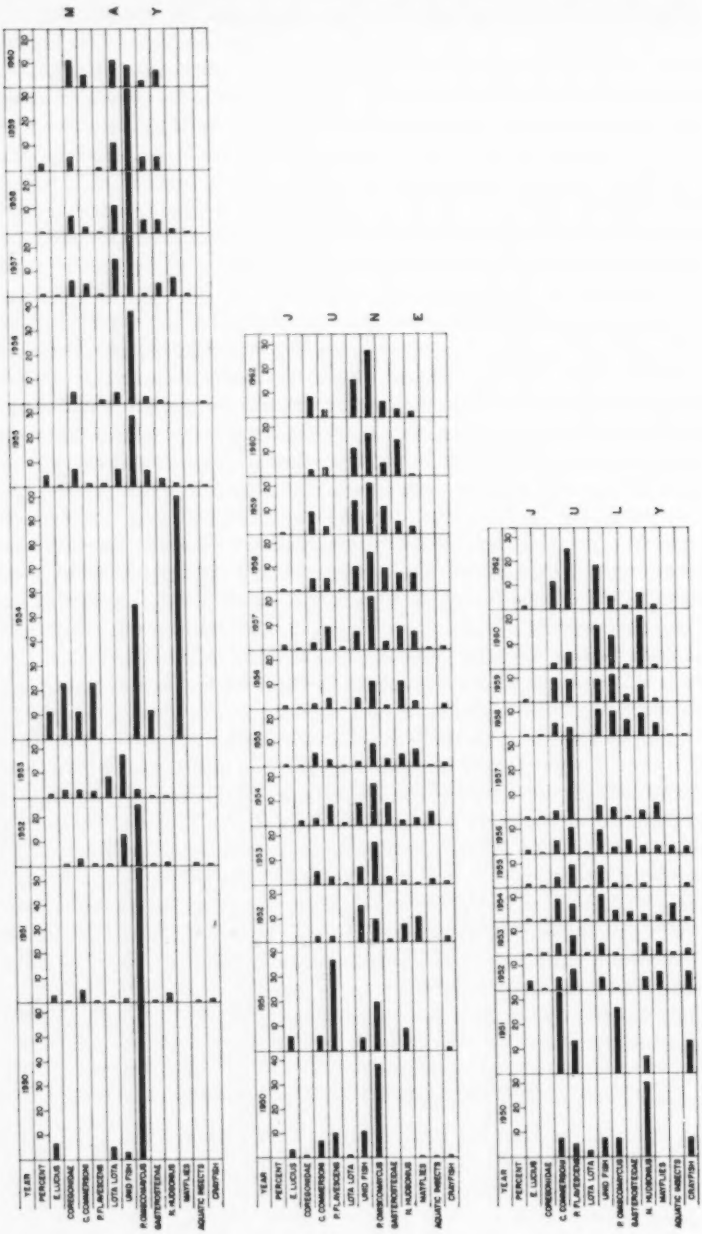
The low frequency of occurrence of perch in 1958 may have been offset by the high frequency of sticklebacks and suckers in that year, as there was no excess of empty stomachs in 1958 which might have indicated a food shortage.

Over the 11-year period of intensive fishing, there did not appear to be any radical changes in the food habits of pike. Those species which served as major food items in the early years continued to be of the same relative importance in later years. The higher frequency of occurrence in some years tended to reflect a higher abundance of the prey itself and thus greater availability to the pike rather than selection by the pike. That the food habits remained fairly consistent is strikingly demonstrated in the case of the sucker where the numbers increased tenfold, yet there was no real increase in their frequency of occurrence in the pike stomachs. Although there were large numbers of these prey extant in the lake, the habits of the predator and prey must have kept them from too close association.

FREQUENCY OF EMPTY STOMACHS

Data collected on Heming Lake pike show that there are not only seasonal, but also annual, differences in the degree of feeding.

The percentage of empty stomachs for each month during the period of investigation is shown in the last line of Fig. 1. During the spring, fall, and winter months there is a higher percentage of stomachs containing food than


MAY
JUNE
JULY
YEAR
PERCENT
E. LUCIUS
COREGONIDAE
C. COMMERSONI
P. FLAVESCENS
LOTA LOTA
UNID. FISH
P. OBESCUMCULUS
BATRACHOTOXIN
H. HUDSONIUS
MINNOWS
AQUATIC INSECTS
CRAYFISH

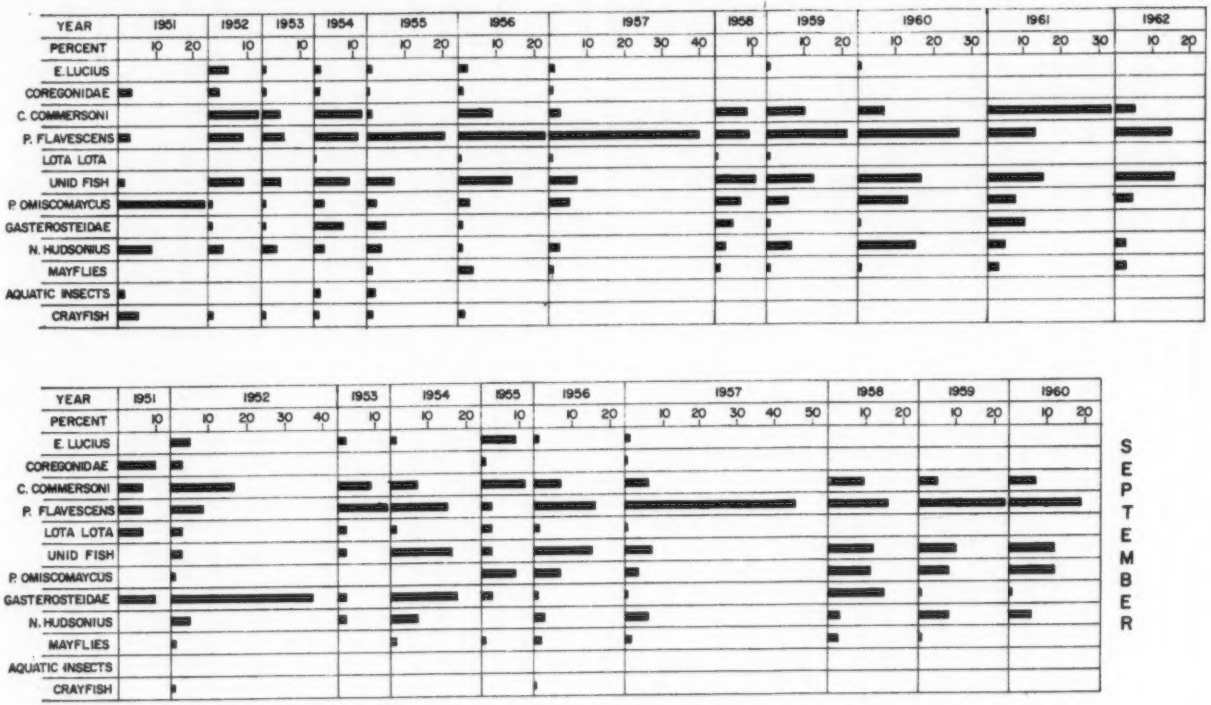


FIG. 2. The frequency of occurrence (%) of the major food items in pike stomachs by month and year for the period 1950–62.

empty, but during the summer months the reverse is true. The highest frequency of empty stomachs is in July. It has been noted (Buss, 1961) that when temperatures rise above an optimum, pike activity is restricted and feeding practically stops. The data from Heming Lake tend to support this hypothesis, as the maximum water temperature occurs during July and this is the month that empty stomachs are most frequently observed. It would appear that sports fishermen also realize that the feeding activity of pike is restricted, as the fishermen do not eagerly seek pike in July.

The percentage of empty stomachs arranged by month and year is shown in Fig. 3. Although there generally is a higher percentage of empty stomachs in June, July, and August than in other months, there are some exceptions. In 1951 there were no empty stomachs in July; however, the sample that month was too small to be of any significance. In 1957 in both June and July there were fewer than 50% empty stomachs, which is an exception to the apparent pattern. In 1960 there were more empty stomachs in May and June than in July and August.

In the years 1952, 1953, 1955, 1956, 1960, and 1962, 50% or more of the stomachs examined were empty. During the period of investigation, there was a marked decrease in the size of the pike and an increase in the number captured. Concomitant changes occurred in the size and numerical abundance of the prey species, particularly in the perch and sucker populations. It is not apparent how such changes could account for the difference in percentage of feeding to nonfeeding pike, as there appeared to be an abundant food supply. Adequate samples were taken monthly so that excessive sampling in midsummer months did not introduce a bias. An examination of annual average water temperatures for May, June, and July provided a possible but not a complete explanation of the difference between years. Assuming that above-average temperatures would restrict feeding activities and lower-than-average temperatures would result in a higher proportion of stomachs with food, positive and negative deviations from the average temperature were obtained. Temperatures were above average for May in 1952, 1955, 1956, 1957, and 1958, for June in 1955 and 1956, and for July in 1954 and 1955. All others during the 8-year period were below average. With the exception of 1953, this temperature relation to feeding held true.

FOOD CONTENT OF PIKE CAPTURED IN GILL NETS AND BY ANGLING

It is a popular belief that pike are more readily caught by angling when their stomachs are empty; however, the following data do not tend to support this view. The stomachs of pike taken by angling were compared with stomachs of pike from gill nets, as it was felt that hunger or fullness should not influence a pike's chances of being caught in a gill net. The number of pike stomachs examined from the two methods of capture are as follows: 1951 — 138 angled, 228 gill-netted; 1955 — 158 angled, 1728 gill-netted. In 1951 there were fewer empty pike stomachs from angled fish (24%) than from gilled fish (38%). This is especially striking as most of the angled fish were caught in May, following

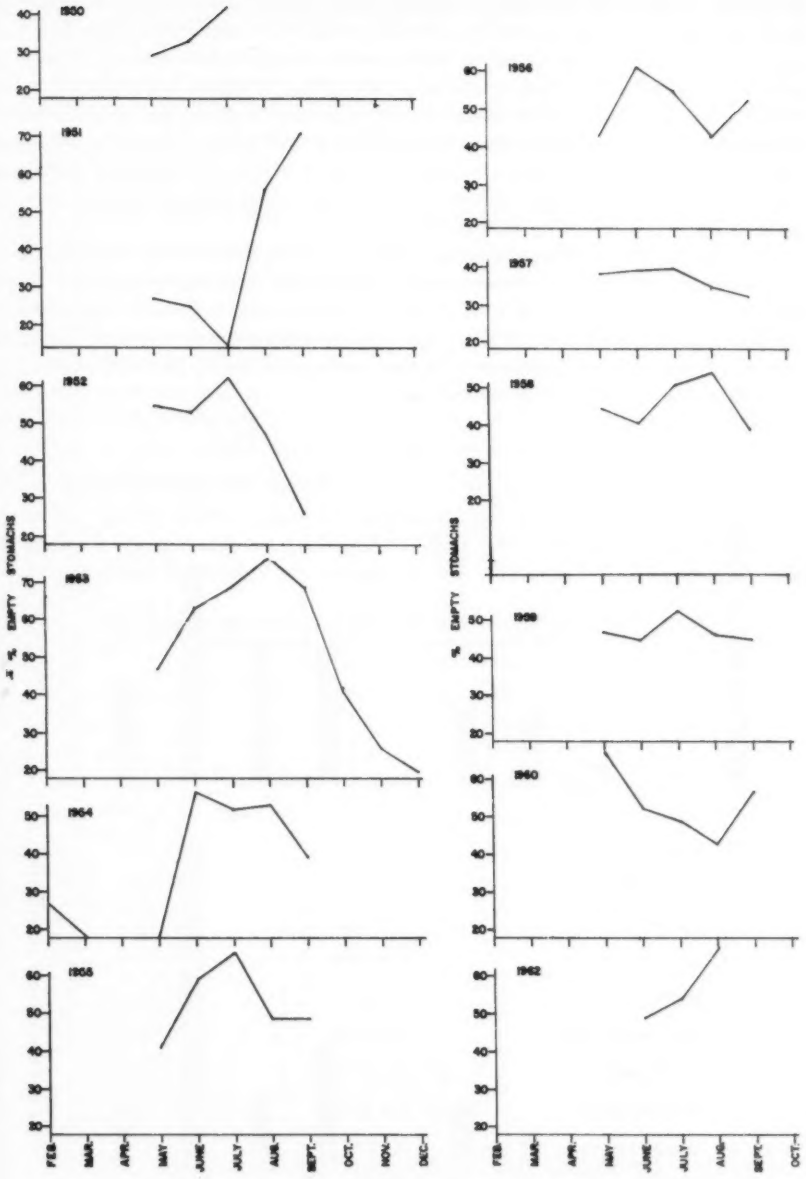


FIG. 3. The number of empty stomachs (%) each month for each year during the period 1950–62.

spawning, and it is generally believed that almost all pike returning from spawning have empty stomachs. There arises the possibility that the pike strikes the lure because of some behaviour pattern rather than from hunger alone. The writer has often seen the same pike in shallow water strike a lure many times as it was pulled back and forth across its path, but never attempt to swallow it. In 1955 there was a high incidence of empty stomachs in angled pike (61%), but the incidence of empty pike stomachs (57%) from gilled fish was also high. Again it has been shown that angled fish differed little in stomach content from fish taken by other means.

The preceding evidence does not refute, but questions the idea that pike with empty stomachs bite more readily than pike with full stomachs, as the comparative data from the two types of fishing gear indicates that at any selected time a percentage of the total pike population will not have any food in their stomachs when examined. The percentage of empty stomachs may vary with the season, as has been shown earlier.

ANALYSIS OF FOOD TYPES BY SEX

A sample (2393) of the 1956 collection of pike stomachs was analyzed to determine if there was any difference in the type and quantity of food consumed by males and females. The data were arranged by months and by sex and the results are shown in Table III. The totals for the combined summer months

TABLE III. Numbers of organisms found in stomachs of male and female pike in 1956. Numbers in parentheses represent number of pike containing food organisms.

	Pike	
Type of food	Male	Female
Pike	18 (18)	15 (15)
Whitefish and cisco	6 (6)	12 (12)
Sucker	85 (56)	69 (47)
Perch	458 (184)	322 (135)
Burbot	6 (6)	13 (13)
Unidentified fish	118 (102)	126 (103)
Trout-perch	361 (72)	348 (59)
Spottail shiner	371 (69)	260 (65)
Mayfly larvae	48 (39)	48 (38)
Crayfish	16 (11)	33 (23)
Empty	651	607

are shown, as there were no obvious differences between months in the types and/or quantities of food organisms consumed. Only the more important food items are listed, as the complete data on the 1956 summer food have already been described. It is readily seen that there are no real differences in food and/or quantities of food eaten by male and female pike; in fact, what is interesting to note is the striking consistency in the numbers of each organism present in the stomachs.

FOOD OF PIKE FROM DEEP- AND SHALLOW-WATER HABITATS

To determine whether area of capture had any influence on type and/or quantity of food consumed by pike, the stomach contents of 2331 pike obtained in the years 1955, 1956, and 1957 from deep and shallow areas are compared (Fig. 4). The pike were captured in gill nets of the same mesh size lifted daily in exactly the same shallow and deep areas of the lake.

More empty stomachs were found in deep-water pike (54%) than in shallow-water pike (46%). The highest incidence of empty stomachs in pike occurred in June from the deep-water catch and in July from the shallow-water catch. The highest percentage of feeding fish for both areas was found in September.

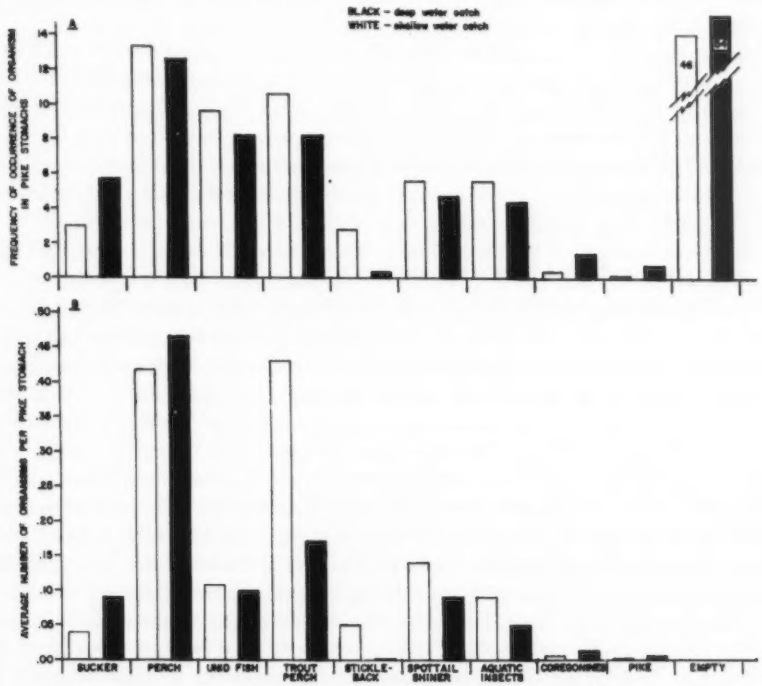


FIG. 4. A. The frequency of occurrence of food organisms in pike stomachs (%) from deep and shallow waters. B. The average number of each food organism per pike stomach from deep and shallow waters.

In both deep and shallow areas the perch is obviously the most important species in the diet of the pike.

The trout-perch and unidentified fish were the next most important food items, and both were present in more stomachs in the pike from the shallow regions than from the deep water. The average number of trout-perch per pike stomach was highest in pike caught in shallow water and was probably the result of heavy predation on them in May–June when they are prevalent in shallow waters.

Spottail shiners and aquatic insects showed the next highest frequency of occurrence and were most prevalent in pike from shallow water. The average number of these organisms is also greater in pike caught in shallow water.

Suckers were found in greatest numbers in pike from deeper waters.

Whitefish and tullibee (*Leucichthys* sp.), important as food items because of their role in the *Triaenophorus* life-cycle, occurred more commonly and were present in greater average numbers in the pike from the deeper habitat. Coregonines (particularly during the summer months) are found in the deeper parts of lakes and therefore are more available to the pike.

Of passing interest is the higher frequency of ducks and mammals in pike stomachs from shallow areas. Mice and shrews, being terrestrial mammals, are more likely to fall in the water near shore and be eaten by a pike.

In summation, it is apparent that there are some differences in the food of pike from deep and shallow areas. There was a higher incidence of empty stomachs in the pike from the deeper water. With the exception of the perch and sucker, the average number of organisms per stomach was greater in the shallow water. How much is eaten appears to depend on the relative abundance of the prey species, and where it is eaten probably depends on the environmental preference of the prey species.

RELATION OF SIZE OF PIKE TO SIZE OF FOOD

The more prominent food items found in stomachs of pike 15 cm and over in length arranged by size intervals are shown in Table IV. The percentage at each length interval was obtained by dividing the frequency of occurrence of the food by the total number of fish in the sample. The trout-perch, a most important food item in pike stomachs, is consumed at about the same level by pike from 15 to 60 cm long, but is markedly less evident in still larger pike. Perch consumption increases with length up to 46 cm and then declines. The incidence of suckers is greater with increasing size and the highest frequency of occurrence is found in pike of 60 cm and greater. Sticklebacks appear to be eaten at approximately the same rate by pike from 15 to 60 cm in length, but are not recorded from larger pike. Spottail shiners are found in greatest numbers in the smaller pike and their frequency of occurrence decreases with increasing length of the predator. Unidentified fish (mainly digested fry and unrecognizable fish remains) and mayflies appear in equal concentrations in pike of moderate size, but are not found in large numbers in pike 60 cm and over in length. Although there were relatively few pike or coregonines found in pike stomachs,

TABLE IV. Food of pike in relation to size (%).

Food	Size of pike (*cm*)			
	15.0–29.9	30.0–44.9	45.0–59.9	60.0 and over
Northern pike	0.2	1.9	6.6	4.2
Lake whitefish	0.1	0.5	0.5	0.0
Tullibee	0.03	0.06	0.2	0.0
Unidentified coregonine	0.02	0.16	...	0.0
White sucker	6.7	11.0	20.0	23.0
Yellow perch	15.3	21.0	10.0	8.3
Trout-perch	25.0	23.0	25.0	2.1
Brook stickleback	7.8	6.6	6.6	0.0
Spottail shiner	20.0	11.0	7.0	2.1
Unidentified fish remains	19.8	18.6	18.0	8.3
Mayflies	5.0	6.2	6.3	2.1
Total number in each size group:	8009	4959	860	48

there is a perceptible increase in the incidence of both between 15 and 60 cm, but a decrease above that size.

The relationship of size of pike to size of prey is illustrated in Fig. 5. As the pike increases in size, there is a corresponding increase in the size of the prey species consumed. The average size of the prey consumed, with the exception of the burbot which does not form a major component of the pike diet, is uniformly similar for the smaller pike.

There are some exceptions to the predator–prey size relationships worth noting — a 38-cm pike had a 46-cm burbot in its stomach, and a 36-cm pike had eaten a 33-cm whitefish.

Three of the important food types in the diet of pike, trout-perch, spottail shiner, and stickleback, are not shown in Fig. 5, as these fish were not measured when found in pike stomachs. As the maximum length of any of these species rarely exceeds 9 cm, it is unlikely that any definitive relationship between length of predator and prey would be evident. The effect of predation on small perch and forage fish is not evident from the preceding data, but as actual counts were made of these fish in the pike gut, it was possible to determine quantitatively the role of these small fish as prey. The average number of each of these organisms is plotted against length of the predator in Fig. 6. For each species there is an increase in the number of fish per pike stomach with increasing length of pike up to a maximum number after which the average number declines.

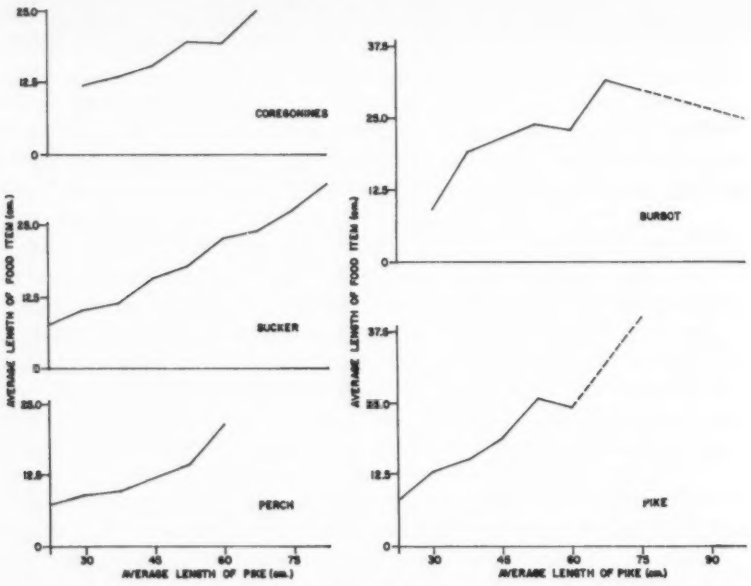


FIG. 5. The relationship between average length of pike and average length of species of fish found in pike stomachs.

Thus, although there is probably little direct relationship between size of predator and size of prey in the case of these small species, there is a definite relationship to the size of predator and number of prey consumed. Perch fry are evident in the diet of pike less than 20 cm long, whereas trout-perch and spottail shiners are not. In pike 10–13 cm long there is a gradual increase in the average number of perch fry consumed, and above that length the consumption increases greatly to a maximum of nine perch fry per pike stomach at lengths between 36–41 cm. Although trout-perch and spottail shiner appear to be important food items for the smaller pike, their incidence in pike stomachs closely resembles that of the perch and the maximum number consumed occurs at lengths greater than 41 cm, which is the upper limit of maximum consumption of perch. It would appear that the small perch were either more abundant or were being selected by the small pike.

The relationship of age of pike to several species of prey fish was determined on a sample of approximately 1850 pike examined in 1957. Perch were eaten by pike ranging in age from 1 to 10 years; however, the major consumption (73%) was by 3-, 4-, and 5-year-old fish. Pike ate pike at ages 2–8, but over 60% of pike consumed were found in 4- and 6-year-old pike. Suckers were prevalent in the diet of several ages of pike between 1 and 9 years of age, but predominated between 3 and 7 years. The coregonines were eaten by pike 4, 6, and 7 years of age. Trout-perch, stickleback, and spottail shiners were eaten mainly by 4-, 5-, and 6-year-old fish.

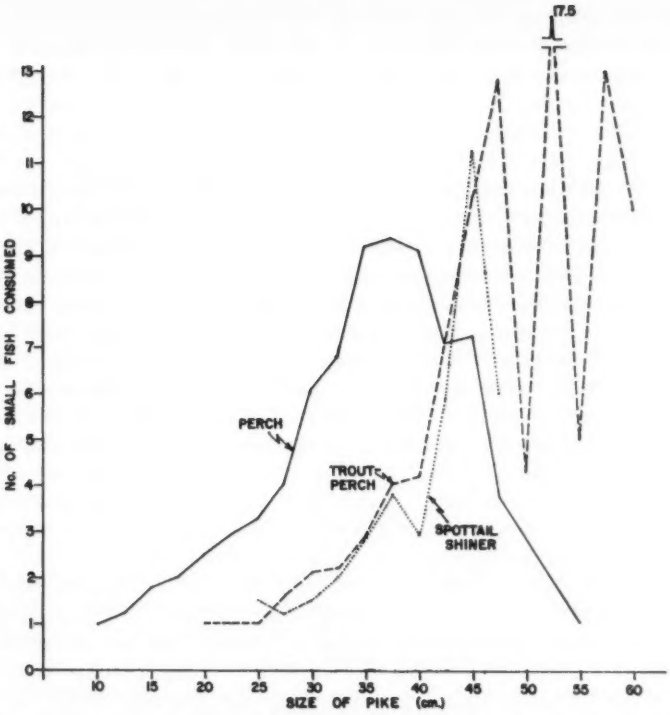


FIG. 6. The average number of small perch, trout-perch, and spottail shiners eaten by pike ranging in length from 10 to 60 cm.

COMPETITION

The predatory species of Heming Lake fish included the burbot and the yellow walleye, as well as the pike. The burbot was never as abundant as pike (1:16 at peak production) and, though the yellow perch was one of the major items in its food (Lawler, 1963), the burbot probably could not be considered a major competitor of the pike for perch because of its relatively low numbers. The preferred habitat of the burbot in deep water probably means that when the burbot is feeding on prey common to both pike and burbot, the pike is feeding on other prey more available in the shallower habitat. The walleye is perhaps the most important direct competitor of the pike, particularly during early spring and fall when it is found inshore, but not so important in the midsummer months when it seeks the deeper, cooler waters. During the early years of the Heming Lake investigation the walleye-pike population seemed well balanced, according to their relative numbers in the gill net catch, and probably exerted equal predatory pressure on the prey species. In the spring of 1954 the spawning walleye population was virtually wiped out when the water level maintained by an ice jam at the mouth of the spawning creek suddenly

dropped and left the fish stranded on the banks of the creek. The walleye population declined after this and to the time of writing has not become re-established at anywhere near its former level.

DISCUSSION

The almost total extinction of one predatory species and the reduction in the average size of another predator, the pike, was accompanied by some apparent changes in populations of other species. Through intensive fishing the average size of the suckers was reduced, but their numerical strength increased about 40% during the last 3 years of heavy fishing. In the period 1950–60 the ratio of pike to sucker in the total catch was 1:2. As suckers were found in only 5.3% of the stomachs of pike during this same period, it would not appear that pike actively "selected" suckers. As shown earlier, the sucker did not appear to be a preferred food of the pike or the burbot, so their increase could probably not be directly attributed to the relaxation of predatory pressure by these species. There has been a striking increase in the gillnet catch of yellow perch since 1955. In the early years of the fishery the perch was present in very small numbers and only rarely were perch over 25 cm found in the catch, perhaps less than a dozen in a year, whereas in the 1958–60 period that many were taken every day. In the period 1950–60 the perch constituted 16% of the total catch of fish and the ratio of pike to perch was 3:2. Perch occurred in 9.2% of all pike stomachs during the same period. Here was a species which has served as a major food in the diet of burbot, of pike, and of walleye, and whose population has actually expanded under the intensive fishery for pike. It should be noted that the increase in the size of the perch population took place while there was still a relatively large walleye population present. The pike population during this period continually increased with increasing fishing pressure, but there was a marked decrease in the average size. The reduction of the predator has had a beneficial effect on at least one species of prey fish. It has been shown that there is a definite relationship between length of predator and length of prey, and that the larger the pike (up to a maximum length of 41 cm) the greater the consumption of perch fry and fingerlings. Some speculation on the potential role of a predator may be made on the basis of an examination of Fig. 6, where it is seen that the larger pike eat more small perch than do the smaller pike. This cannot be strictly a matter of selection for size, but rather must be for a volume of food required to provide for metabolism and growth. It has been suggested that 3–5 lb (135–225 dkg) of fish are required to produce 1 lb (45 dkg) of pike. If a 41-cm pike, average weight of 1 lb, is feeding on small perch at the 3:1 rate, approximately 735 small perch would have been required to produce the 1 lb of fish. It is obvious that the medium-sized pike can be considered serious predators on young year-classes of perch.

The effect of the predator (pike) on populations of other small forage fishes (trout-perch, spottail shiners) is not known, because of the lack of quantitative data on their population size; however, at maximum predator

density it is likely that some effect could be measured, as these fish appear in the gut of medium to large pike in very great numbers when available.

The continuation of the life-cycle of *T. crassus* does not appear to depend on the consumption of large quantities of coregonine fish by pike, as these fish were present in very small amounts in the diet during the study. The higher incidence of coregonines in the diet did occur in the late fall when the infestation for the year would be well established in the flesh of the fish, thus making optimum numbers of the parasite available to the final host, the pike.

From the analysis of the feeding habits of the pike in Heming Lake, it would appear that relative abundance and seasonal availability determine the incidence of prey consumed. There is a positive relationship between the size of pike and the size of the prey, and there is further evidence that among the small prey there is a positive relationship between the number of prey consumed and size of predator. It would appear that the reduction of the average size of the pike has had an effect on the survival of other fish species, and that predation can be considered a major factor influencing the abundance of a species and its population properties.

ACKNOWLEDGMENTS

I wish to express my thanks to the many people who have helped in the collection of samples and data. Special acknowledgment is due to G. P. McRae, R. S. Williams, and J. H. Martin who assisted in the routine collection and tabulation of the data, and to S. T. Zettler for the painstaking preparation of the many figures.

The constructive criticism of the manuscript by Drs W. A. Kennedy and G. F. M. Smith is sincerely appreciated.

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Influence of Photoperiod on Growth of Green Sunfish, *Lepomis cyanellus*[1,2,3]

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ABSTRACT

Four 6-week experiments were conducted to evaluate the effect of photoperiod on growth (total length and weight), food consumption, and food conversion efficiency by green sunfish. Fish were held at constant temperatures in light-tight aquaria under four photoperiods (8-hr constant; 16-hr constant; variable, increasing from 8 to 16 hr; and variable, decreasing from 16 to 8 hr).

Growth, food consumption, and food conversion efficiency were all influenced by photoperiod. Food consumption varied directly with the amount of light to which fish were exposed. Fish growth and food conversion efficiency were closely correlated and were generally highest in the increasing, lowest in the decreasing, and intermediate in the two constant photoperiods, but higher in the longer daylength. The results suggest that photoperiod influences growth through increasing conversion efficiency and also possibly through stimulating food consumption.

Varying daylength exerts a greater influence on fish growth than a constant daylength. Increasing photoperiod stimulates growth and decreasing photoperiod inhibits growth. This result suggests that the lack of growth of warmwater fish in fall when water temperatures and average daylength correspond to those of spring is largely due to the influence of decreasing daylength.

INTRODUCTION

Seasonal growth cycles of fish have usually been attributed to seasonal changes in temperature because of the relationship between temperature and the growth rate of poikilotherms. In temperate regions, however, annual cycles of photoperiod and temperature are nearly in phase and the individual effects of these two factors are difficult to distinguish in the natural environment.

Past studies involving light and fish growth have yielded conflicting results. Brown (1946) demonstrated an inverse relationship; both Anderson (1959) and Bjorklund (1958) showed no relationship between daylength and growth. Two studies which demonstrated a direct relationship (Eisler, 1957; Tryon, 1943) compared growth of fingerlings (chinook salmon and cutthroat trout, respectively) reared in darkness or in light. In contrast, studies of mature goldfish (Bjorklund, 1958) indicated greater growth in darkness which was attributed to lack of activity.

These studies, Tryon excepted, compared groups of fish subjected to different but constant daylengths. Various studies (Hoover and Hubbard,

[1]Received for publication January 18, 1965.
[2]Published with the approval of the director of the Michigan Agricultural Experiment Station as Journal Series No. 3244.
[3]This paper is based on a thesis submitted by W. L. Gross in partial fulfilment of the requirements for the Master of Science degree in Fisheries and Wildlife, Michigan State University.

J. Fish. Res. Bd. Canada, 22(6), 1965.
Printed in Canada.

1937; Hazzard and Eddy, 1951; Allison, 1951) have shown that daily changes in daylength affect the reproductive system, but varying daylength has not been studied in relation to growth. Swift (1961) noted that it is important to distinguish between the effect of day-to-day changes in daylength and the effect of daylength when it is constant each day, but did not compare the two factors.

This study was undertaken to determine if fish growth is influenced by daylength when temperature is constant and to compare constant and varying daylengths.

METHODS

Green sunfish (*Lepomis cyanellus*, Rafinesque), from 2 to 4 years old and from 68 to 110 mm in total length, were brought into the laboratory at least 1 month prior to each of the four 6-week experiments. In each of the first three experiments, 30 fish were randomly assigned to compartments (10 fish per compartment) of an aquarium with one of the following light conditions: (1) constant 8-hr; (2) constant 16-hr; (3) increasing daylength, 8 to 16 hr; (4) decreasing daylength, 16 to 8 hr. In the fourth experiment, 15 fish (5 per compartment) were held in an aquarium with each of the above photoperiods. Daylength in the varying photoperiods was changed approximately 12 min each day by adjustment of electric timers.

Individual experiments were conducted during the following periods: (1) August–September, (2) July–August, (3) October–November, and (4) February–April. Fish were subjected to light conditions prevailing in the laboratory when first collected. Acclimation to a given photoperiod and performance of an experiment were conducted in light-tight, 100-gal aquaria illuminated by 30-w, cool-white fluorescent tubes installed approximately 8 inches above the water surface. Prior to the start of an experiment, fish were acclimated to the photoperiod at which they would begin the experiment, except in the first experiment when all fish were acclimated to a 12-hr photoperiod. The acclimation period was 3, 3, 1, and 4 weeks, respectively, for the four experiments.

Water temperatures varied only slightly in the four experiments depending upon the room temperature. The median temperature for the four experiments was 78, 77, 77, and 74 F in respective order. Variations among aquaria at any one time were infrequent with a maximum deviation of 2 F degrees between any two aquaria. One aquarium was never consistently warmer or cooler than another.

Fish were fed to satiation for ½ hr each day. Excess food was removed by siphon and weighed to permit determination of food consumption and food conversion efficiency. Estimates of these parameters were based upon the total weight gain and food intake of all fish under each photoperiod because the amount of food consumed by individual fish was not known. Food consumption was expressed in terms of per cent body weight to compensate for differences resulting from variations in size of fish under different photoperiods. Food conversion efficiency refers to the weight gain per unit of food intake multiplied

by 100 (Table IV). It represents the "gross efficiency" (Brown, 1956) of food utilization because it includes that weight of food which is required for maintenance.

Lengths and weights of fish were recorded at the beginning, midpoint, and end of an experiment after anesthetizing the fish and blotting them to remove excess moisture. Calculating growth in terms of per cent initial weight or length did not alter the ranking of the various photoperiods regarding overall gains in length and weight, indicating the effect of initial size was negligible. Therefore, the data are reported in terms of actual gains in weight and length.

Since there was some variation in methods between experiments, we employed nonparametric statistics (Siegel, 1956) in analyzing the data, assuming the data reflected no more than an ordinal scale of measurement. Under these circumstances, we are concerned only with the relative gains attained by photoperiod groups within a particular experiment in which conditions were constant.

RESULTS AND DISCUSSION

Growth in Length and Weight

In analyzing the influence of photoperiod on growth, only the average gains in length and weight of fish under each photoperiod of each experiment were considered (Table I). A Friedman Rank Sum Test (Siegel, 1956) showed the four photoperiod groups significantly different with respect to weight gain ($P < .05$) but not significantly different in total length gain ($P < .40$). The greater weight gain by fish exposed to the longer light periods (increasing and 16-hr groups) demonstrates a direct relationship between daylength and growth. Since fish were also measured at the midpoint of a 6-week experiment, fish growth during the first and second 3-week periods under varying daylength conditions was also compared. Examination of these data (Table II) also indicates this direct relationship particularly with respect to weight.

Our results agree with those of Eisler (1957) and Tryon (1943) although the experiments are not strictly comparable. The results disagree with the work of Bjorklund (1958); however, he fed his fish a limited amount of food (about 1.7% of the body weight daily) and the increased activity of fish in the longer photoperiod undoubtedly reduced the growth rate. Fish with an adequate or unlimited food supply could compensate for the additional energy expenditure by increasing their food consumption and therefore equal or exceed the growth of fish in a shorter photoperiod.

Fish growth is influenced by the type of daylength (constant or varying daylength) employed in photoperiod studies. Fish generally grew better in the 16-hr than in the 8-hr constant daylength, but the difference in growth was not statistically significant for total length ($P > .10$) and marginally significant with respect to weight ($P = .10$) using the Mann-Whitney U Test (Siegel, 1956). However, greater differences in growth were noted between increasing and decreasing daylength. The same statistical test showed a significant difference in both length gain ($P < .05$) and weight gain ($P < .05$) between the

TABLE I. Average gain in total length and weight of fish by experiment and photoperiod; the rank of photoperiod groups in each experiment and rank sums over all experiments.

Experiment	8 hr	Rank	8–16 hr	Rank	16 hr	Rank	16–8 hr	Rank
	Gain in total length (*mm*)							
1	6.81	II	8.00	III	9.55	IV	6.46	I
2	9.45	IV	8.32	III	6.53	II	5.84	I
3	3.43[a]	I	8.21	IV	6.63[a]	II	6.76	III
4	9.43	I	11.86	IV	10.20	II	10.73	III
Rank sum		8		14		10		8
	Gain in weight (*g*)							
1	3.76	II	4.50	III	6.74	IV	2.90	I
2	4.12	III	4.59	IV	3.83	II	2.09	I
3	0.63[a]	I	3.16	IV	2.76[a]	III	2.17	II
4	5.10	I	7.08	IV	6.52	III	6.30	II
Rank sum		7		15		12		6

[a]Reduced growth believed due to fouled water supply during part of experiment.

TABLE II. Average gain in total length and weight of fish under varying photoperiods by 3-week periods. Footnotes indicate significant differences between 3-week periods according to Sign Test.

Photoperiod	Gain in total length (*mm*)		Gain in weight (*g*)	
	First 3 weeks	Second 3 weeks	First 3 weeks	Second 3 weeks
8–16 hr	4.71	4.39	1.99	2.85[a]
16–8 hr	4.76	2.69[b]	2.60	0.77[c]

[a]P = .073.
[b]P = .019.
[c]P = .001.

two varying daylength groups. The effect of changing daylength on fish growth is perhaps best demonstrated by comparing growth of fish in the first 3-week period of the increasing group with the second 3-week period of the decreasing group (Table II). Both groups were exposed to the same amount of light (8–12 hr and 12–8 hr, respectively) but fish exposed to increasing daylength gained 2.5 times as much weight as those exposed to decreasing daylength, suggesting a stimulative effect of increasing and an inhibitive effect of decreasing daylength.

To further evaluate this action of varying daylength, we extended the fourth experiment an additional 3 weeks, maintaining the daylength attained by all groups at the end of the 6-week experiment (the 8-hr and 16-hr constant daylengths remained unchanged, the decreasing group was continued at 8 hr and the increasing group at 16 hr of light per day). Growth of the various groups (Table III) was compared using the Mann-Whitney U Test. The significant difference in growth between the two 8-hr groups (total length, $P < .01$, weight, $P < .001$) and between the two 16-hr groups (total length, $P < .05$, weight, $P < .05$) attest to the stimulative and inhibitive effects of prior increasing and decreasing daylengths. The data also demonstrate an influence of prior photoperiod history on fish growth.

The failure of other studies to show a direct relationship between daylength and growth may in part be due to use of constant daylength conditions. Daily changes in daylength exert a stimulative or inhibitive effect which is not apparent when constant daylengths are employed. It appears that photoperiod studies should be conducted using varying daylength conditions.

TABLE III. Average gain in total length and weight of fish under each photoperiod for the third 3-week period of the fourth experiment.

Description of group	Gain in total length (*mm*)	Gain in weight (g)
Group 8C — constant 8-hr during entire experiment	4.29	3.21
Group 8V — constant 8-hr, previously decreasing (16–8)	1.93	0.43
Group 16C — constant 16-hr during entire experiment	3.07	1.93
Group 16V — constant 16-hr, previously increasing (8–16)	4.86	3.62

Brown (1946) observed an endogenous seasonal growth pattern in brown trout held under uniform light conditions throughout the year. Our experiments with green sunfish, performed at various times of the year, exhibited reasonably consistent results between experiments and provide no evidence of an endogenous seasonal cycle.

Food Consumption and Food Conversion Efficiency

Food consumption and food conversion efficiency were determined in search of a possible mechanism through which photoperiod influences growth. One previous photoperiod study involving food consumption measurements (Anderson, 1959) indicated no difference between the amount of food consumed by bluegills held at 10-hr and 15-hr daylengths. Our data (Table IV) not only show significant differences in food consumption between photoperiods (by the Friedman Rank Sum Test, $P = .033$), but a direct relationship between food

TABLE IV. Average food consumption (*above*) and efficiency of food conversion (*below*) of green sunfish by experiment and photoperiod, and the rank of corresponding values in each experiment.

Experiment	8 hr	Rank	8–16 hr	Rank	16 hr	Rank	16–8 hr	Rank
Food consumption (as per cent of body weight)								
1	38.78	I	42.64	II	57.24	IV	44.67	III
2	83.70	III	77.06	II	87.11	IV	67.60	I
3	76.55	I	91.70	III	103.01	IV	79.05	II
4	44.35	I	55.15	II	58.74	IV	55.74	III
Rank sum		6		9		16		9
Food conversion efficiency $\left(\frac{\text{wt gain in grams}}{\text{food consumed in grams}} \times 100\right)$								
1	57.05	II	59.25	III	68.72	IV	41.03	I
2	26.60	III	28.59	IV	23.94	II	17.11	I
3	7.44	I	23.48	IV	20.97	II	21.63	III
4	70.73	II	82.38	IV	74.16	III	63.27	I
Rank sum		8		15		11		6

consumption and average daylength. Fish exposed to varying photoperiods consumed more food during the 3-week period with longer daylengths.

Under laboratory conditions, it appears that most fish are more active in the light than in the dark. Bjorklund (1958) attributed greater growth of goldfish held in darkness than in light to decreased activity. Anderson (1959) observed that bluegills are normally quiescent and rest on the bottom during periods of darkness. Consequently, maintenance requirements of fish increase as daylength increases. Increased maintenance requirements may be satisfied by increasing food consumption or decreasing conversion efficiency. In our experiments, food consumption was related to the average amount of light; therefore, it appears that even though fed only once daily, these fish compensated for increased energy requirements by consuming more food. The extent that this increased activity affected food consumption is unknown, but the interrelationships among photoperiod, food consumption, and growth suggest that the influence of photoperiod on growth may be partially effected through stimulating food consumption in fish.

Not only did fish consume more food during longer daylengths, but their efficiency of food conversion was higher than for shorter days (Table IV). The Friedman Rank Sum Test showed significant differences between photoperiods ($P = .068$) with the highest efficiency in the increasing and 16-hr daylengths. Again, in comparing the two 3-week periods of the varying photoperiods,

efficiency was greater during the longer portions of each photoperiod. Assuming that differences in maintenance requirements of fish were satisfied by changes in food intake, these data suggest that the effect of photoperiod is also mediated through increased conversion efficiency.

Summarizing all the above data in the form of rank sums (Table V), certain relationships between photoperiod and the various parameters become apparent. Food consumption during the 6-week periods was closely related to the average amount of light, as borne out by the high ranking of the 16-hr day, the intermediate and equal ranking of the varying photoperiods, and the low ranking of the 8-hr day. But, efficiency of food conversion was influenced by the daily distribution of light within the 6-week period, as indicated by the highest rank sum of the increasing and lowest rank sum of the decreasing photoperiods — both groups having received an equal amount of light. Growth was more closely correlated to food conversion efficiency than to food consumption.

TABLE V. Summary of rank sums by parameter and photoperiod, and probability for significance tests by the Friedman Rank Sum Test.

	8 hr	8–16 hr	16 hr	16–8 hr	P
Growth (total length)	8	14	10	8	.30
Growth (weight)	7	15	12	6	.05
Food consumption	6	9	16	9	.05
Conversion efficiency	8	15	11	6	.10

How photoperiod may influence food conversion efficiency is unknown, but it is probably an indirect effect ultimately involving regulation of metabolic activity by the endocrine system. The existence of a specific growth hormone secreted by the fish pituitary gland has been established (Hoar, 1957). Growth hormone is an important regulator of protein synthesis in mammals and most probably serves this same function in fish. Swift and Pickford (1962) have described a seasonal variation in the level of growth hormone in the perch pituitary. That the pituitary is affected by photoperiod is well demonstrated by many experiments (reviewed by Pickford and Atz, 1957) involving light manipulation and production of gonadotropic hormones. The observed relationship between photoperiod and conversion efficiency may reflect differences in protein synthesis brought about by photoperiod control of growth hormone production (via the pituitary). It is possible that mechanisms concerned with lipid deposition are also involved. Changes in the protein and lipid content of the fish were not studied and it is not known whether the observed growth was the result of either increased protein synthesis, lipid synthesis, or both.

Our data demonstrate an interaction between photoperiod and fish growth. This interaction is difficult to observe under natural conditions because the

weaker photoperiod effect generally compliments the stronger temperature effect. In the seasonal growth cycle, the rapid growth by fish in spring (April–June) may be the result of a synergistic action of both increasing temperature and daylength. Continued good growth during July and part of August may involve warm temperatures and the influence of a prior history of increasing photoperiod. Decreasing temperature and daylength would account for the rapid decrease in late fall (October and November). The lack of growth in winter is undoubtedly due more to temperature than reduced daylength or the lasting influence of decreasing daylength. Our data relating to differences in growth between increasing and decreasing photoperiod groups provide a plausible explanation for the lack of growth among warmwater fish in early fall when temperatures and average daylength correspond to those of the spring season.

ACKNOWLEDGMENTS

The authors wish to thank Mr Kenneth J. Linton for his review of the statistical procedures and the manuscript. This project was supported in part by grant G-10757 from the National Science Foundation.

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Parasites as an Auxiliary Source of Information About the Biology of Pacific Salmons (Genus *Oncorhynchus*)[1,2]

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ABSTRACT

The value of data from parasitology in providing supplementary information about the food and feeding habits, the associated fauna (other than food organisms) in the freshwater habitat, the ocean distribution of specific stocks, the "homing" phenomenon, and the freshwater origin of anadromous Pacific salmon is demonstrated.

INTRODUCTION

The composition of the parasite fauna of a species of fish depends upon two sets of factors. First are the ecological factors, encompassing the biotic and abiotic characteristics of the fish's habitat(s), which determine the opportunities for contact between parasite and host. Second are the evolutionary factors, the accumulation of physiological and morphological adaptations of the parasite and host which permit the parasite to remain associated with the host and continue its development.

The relative importance of the physiological and morphological adaptations, as compared with ecological adaptations, in the establishment of specific parasite–host relationships is frequently difficult to measure in the absence of experimental data. There is no doubt, however, that some fish parasites are so highly specialized physiologically or morphologically that they are able to develop in only a few phylogenetically related fishes or they may be restricted to even a single species of fish. Other parasites are obviously relatively unspecialized and may be found in a wide variety of unrelated families or even orders of fishes. In such cases ecological factors play a prime role in dictating the host, as well as the geographical, distribution of the parasite.

When the factors responsible for enabling a particular parasite species to establish itself within or on a fish are known, then certain features of the biology of the infected host may be inferred from the presence of the parasite. Not only can parasites be of assistance in shedding light or providing supplementary evidence on present-day aspects of the biology of an individual, stock, or species of fish, but, because parasites are evolving along with their hosts, although generally at a slower rate, they also may provide clues regarding the history of a species or higher taxon of fishes.

With these few general remarks in mind the parasite fauna of Pacific salmons will be examined to see in what ways the parasites reflect the present

[1]Received for publication April 23, 1965.
[2]Based on a contribution to a symposium on Parasites of Fish at the 16th meeting of the Canadian Committee on Freshwater Fisheries Research, Ottawa, January 7, 1963.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

and past modes of life of their hosts. Much of this faunal information was obtained during recent extensive studies carried out at this Station and is on Station files. In what follows, where no specific reference to source of data is given, it is to be understood that this "file data" is the source. (These data are currently being prepared for publication.)

FOOD AND FEEDING HABITS

More than 100 species of parasites have been recorded from Pacific salmons. About 85% of them are internal parasites (endoparasites), most of which inhabit the digestive tract. With some exceptions, notably myxosporidian protozoa and the metacercarial stage of trematodes, these endoparasites are acquired by the salmon through feeding on infected intermediate hosts. As the variety of animals used as intermediate hosts of each parasite species is usually more or less restricted, the general nature of the food of the fish can be deduced from the endoparasites it harbors. Some examples follow.

The freshwater parasites *Philonema oncorhynchi*, a nematode, and larval *Diphyllobothrium* sp. (?spp.) and *Proteocephalus* sp. (?spp.), two genera of tapeworms, occur commonly in sockeye salmon. These parasitological characteristics reflect the importance of planktonic copepods in the diet of young sockeye salmon during their lake residence, since the three parasites utilize cyclopid and/or diaptomid copepods as hosts of the larval stages infective for salmon. The feeding of young sockeye salmon, however, is not entirely confined to planktonic organisms. Certain parasites which use mayfly larvae (*Ephemera*, *Hexagenia*) and/or amphipods (*Gammarus*, *Pontoporeia*) as intermediate hosts, such as the trematode *Crepidostomum farionis* and the nematodes *Metabronema salvelini* and *Cystidicola farionis*, sometimes are found in seaward migrant sockeye salmon. Thus, these arthropods, which live along the shores of lakes or in streams, at times form part of the diet of young sockeye salmon.

The incidence of *Crepidostomum farionis* and *Metabronema salvelini* generally is considerably higher in coho salmon smolts (*Oncorhynchus kisutch*) than in sockeye salmon smolts, whereas the reverse situation occurs with *Diphyllobothrium* sp., *Proteocephalus* sp., and *Philonema oncorhynchi*. These facts indicate that there are considerable differences between the diets of young coho and sockeye salmon.

The limited feeding in fresh water of the fry of pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon, which generally embark on their downstream migration immediately after emerging from the gravel, is reflected in a general paucity of freshwater parasites in these two species of salmon. Such food as has been reported to occur in their stomachs consists mainly of larval insects and other stream bottom forms, such as ostracods and harpacticid copepods (Dvinin, 1959; Levanidov and Levanidova, 1957; McDonald, 1960; Synkova, 1951). Parasitological data indicate that they must, at least in some areas, also consume some planktonic copepods, which are probably carried downstream passively with the flow of water from lakes. The evidence is provided by the occasional finding of *Philonema oncorhynchi* in adult pink and

chum salmon (Akhmerov, 1954, 1955; Fujita, 1939, 1940; Mamaev *et al.*, 1959; also "file data") and of the plerocercoid larva of *Triaenophorus crassus* in adult chum salmon (Uzmann and Hesselholt, 1957), the infected fish having been caught at sea or in estuaries. Since both parasites are of freshwater origin, the pink and chum salmon must have become infected during their short early life in fresh water, by ingesting cyclopid or diaptomid copepods, the intermediate hosts of these parasites.

Once the young salmon (all species) reach the sea they gradually lose their external and most of their internal parasites acquired in fresh water, and begin to accumulate a new set of parasites from the marine environment. A few species of endoparasites, principally those which live in organs or regions other than the lumen of the gut, may live as long as the salmon, e.g. *Philonema oncorhynchi* which occurs in the adult stage in the body cavity, *Diphyllobothrium* sp. plerocercoid larvae which occur in cysts attached to the stomach serosa, and *Triaenophorus crassus* plerocercoids which occur in the musculature.

The parasites acquired in the sea by pink and sockeye salmon suggest that both species, during their marine life, feed on planktonic crustacea and to a lesser extent on fish. Indicative of the consumption of crustacean plankters are the very common trematodes *Lecithaster gibbosus* and *Brachyphallus crenatus*. The presence of the trematode *Bucephaloides basargini* speaks of the piscivorous habits of these two species of salmon.

Although the array of marine species of parasites occurring in sockeye salmon and that occurring in pink salmon is very similar, there are differences between these two salmons in the frequencies and/or intensities of infections with some parasites. Some of these differences point to dissimilarities in the feeding habits of pink and sockeye salmon. For example, *Bucephaloides basargini* is more frequently encountered in pink salmon than in sockeye salmon, implying a greater importance of fish in the diet of pink salmon. This dietary difference has been confirmed by direct analysis of stomach contents (Allen and Aron, 1958; Andrievskaya, 1957).

Parasites also show that in different oceanic regions the same species of salmon may feed predominantly on different organisms. Off the east and west coasts of the Kamchatka Peninsula of the USSR, immature specimens of the acanthocephalan *Echinorhynchus gadi* are commonly encountered in the intestines of sockeye salmon, whereas this species occurs rarely in sockeye salmon captured in other areas, including along the North American coast. This is not due to the parasite, *per se*, having a limited distribution. On the contrary, *E. gadi* is widely distributed in all northern seas and basically is a parasite of fishes of the cod family (Gadidae), although it has been recorded from many other, especially demersal, fishes. It is a common parasite of cod (*Gadus macrocephalus*) in Kamchatkan (Zhukov, 1960; Strelkov, 1960) and British Columbia waters (Margolis, unpublished data). Since its intermediate hosts are amphipods it appears that sockeye salmon feed more heavily on amphipods in Kamchatkan waters than they do elsewhere.

It has been an accepted view that salmon cease feeding upon re-entry into fresh water on their spawning migration. Data from our parasite studies reveal that there are exceptions to this general phenomenon. Usually the only new parasites acquired by adult salmon after they leave the sea are those with a direct life cycle and which actively attack the fish (i.e. they are not introduced passively with food organisms), such as species of the ectoparasitic copepod genus *Salmincola* and trematode larvae (metacercariae) of the family Strigeidae. However, almost 400 small specimens of the freshwater trematode *Crepidostomum farionis*, a number of which were immature, were found in the intestine of a male sockeye salmon taken from Issaquah Creek in the State of Washington. This fish obviously had recently fed quite intensively in fresh water to amass this large number of young trematodes. The presence of marine parasites (*Anisakis* sp. larva, *Phyllobothrium caudatum*, and *Tubulovesicula lindbergi*) in the same fish is evidence that it was a migratory and not a "resident" sockeye salmon. The infection with *Crepidostomum* could not have been a carry-over from the smolt stage because the life span of the trematode in sockeye salmon must be less than 2 years, as evidenced from the fairly high incidence of *C. farionis* (some of which were immature specimens) in Ugashik River (western Alaska) seaward migrants and the absence of this trematode in sockeye salmon returning to spawn in the Ugashik system after 2 years at sea; the Issaquah sockeye salmon, judging from its size (fork length 54 cm, weight 4.75 lb or 2.15 kg), had been at sea for at least 2 years.

Although many others could be mentioned, these examples are sufficient to show the relationship between parasites and the feeding habits and food of salmon.

ASSOCIATED FAUNA

Parasites also provide evidence of the presence of specific animals in the biocoenosis of the fresh waters inhabited by salmon, but which do not constitute part of the salmon's food. The parasites of this group comprise two categories. To one of these belong the parasites with a direct life cycle which are primarily parasites of another fish and only secondarily invade salmon. To the other belong parasites with a three-host life cycle which utilize salmon as second intermediate hosts, with the first intermediate or final host being restricted to a single species.

The ectoparasitic copepod *Ergasilus auritus* serves as an example of the first category. This copepod is a common parasite of the three-spined stickleback (*Gasterosteus aculeatus*), but it may sometimes be found on young sockeye salmon (Roberts, 1963). It occurs on sticklebacks in areas where sockeye salmon are not present, but the reverse situation is not known to occur. Thus, the presence of *E. auritus* on the gills of young sockeye salmon indicates that they are living in close association with sticklebacks. As examples of the second category we may cite the parasites *Triaenophorus crassus* and *Nanophyetus salmincola*. *Triaenophorus crassus* matures only in the gut of pike. Consequently, pike must be present in lakes where young sockeye have been found to harbor

the plerocercoid larvae in the musculature, namely in certain areas in western Alaska (Margolis, 1963). The first intermediate host of the trematode *Nanophyetus salmincola* is the snail *Oxytrema silicula*. The second intermediate hosts are various salmonids (including species of *Oncorhynchus*) in which the parasite encysts in a variety of tissues, and the final hosts, in which the adult trematode develops in the intestine, are several species of carnivores (Pratt and McCauley, 1961, and references therein). The occurrence of infected salmonids in certain areas of northern California, Oregon, and Washington indicates the presence of the snail *Oxytrema silicula*.

OCEAN DISTRIBUTION

Perhaps the most noteworthy contribution of parasitology to an understanding of the life of salmon has been in the use of parasites to determine the ocean distribution of some stocks of sockeye salmon (Margolis, 1963). To fulfil the role of a "biological tag" a parasite must have a relatively long life span, preferably as long as that of the fish, and, of course, the areas in which infection take place must be limited. Two parasites of freshwater origin have been found in sockeye salmon which satisfy these requirements. Others of potential value are presently under study.

The two freshwater parasites are the plerocercoid larva of *Triaenophorus crassus*, which occurs in the somatic musculature, and the adults of the nematode *Dacnitis truttae*, which occurs in the intestine.

As has been noted already the presence of *T. crassus* larvae in sockeye salmon is dependent upon the co-existence of sockeye salmon and pike, the definitive host of this tapeworm, in the same lake system. These two species of fish are known to occur together only in some lakes of western Alaska, and extensive sampling over a period of 5 years has confirmed that *T. crassus* is found in downstream migrant sockeye from some western Alaskan river systems only and in adults returning to spawn in these systems. Since the parasite cannot be acquired once the fish enter the sea, *Triaenophorus*-infected sockeye salmon captured at sea must be of western Alaskan, or essentially Bristol Bay, origin, because sockeye production in western Alaska north of Bristol Bay is negligible.

Dacnitis truttae, on the other hand, is known to occur only in some sockeye salmon from rivers on both the east and west coasts of Kamchatka. It has not been found in extensive sampling of sockeye salmon smolts and adults from North America. The life history of this nematode is unknown. Hence, the reasons for its failure to appear in North American sockeye salmon are obscure. The occurrence of *D. truttae* in sockeye salmon which have spent as much as 4 years at sea indicates that some specimens may live as long as this host.

In Fig. 1 the ocean distributions of Bristol Bay and Kamchatkan sockeye salmon as identified by the presence of *Triaenophorus* and *Dacnitis*, respectively, are shown. In this figure, data obtained from sampling from 1955 to 1959, inclusive, have been combined. The upper chart represents maturing sockeye salmon, that is fish which would have returned to spawn in the year they were

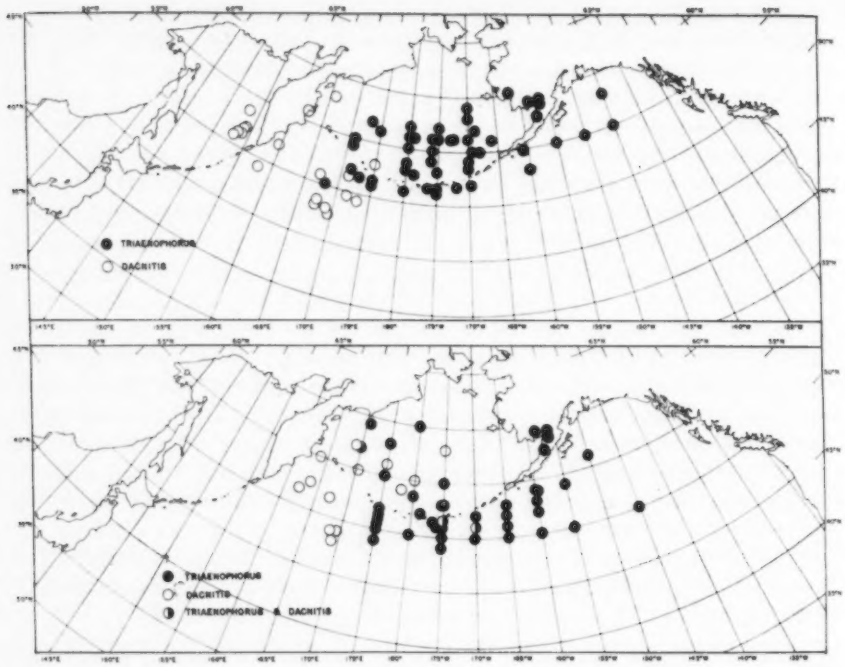

FIG. 1. Distribution of *Triaenophorus*-infected and *Dacnitis*-infected sockeye salmon. Upper chart: maturing fish; lower chart: immature fish. (Based on fig. 21 and other data in Margolis, 1963.)

caught, and the lower chart represents immature sockeye salmon, that is fish which would have remained at sea for at least 1 or more years before returning to fresh water to spawn. The maturing sockeye salmon were taken mainly from mid May to the end of June, whereas the immatures were caught mainly in July and August.

Both the maturing and immature Bristol Bay sockeye salmon show an extensive westward and eastward distribution covering an ocean expanse of more than 1700 miles in latitude and about 700 miles in longitude. In terms of the distance from Bristol Bay both groups of sockeye salmon have migrated as much as 1100–1200 miles to the east and west.

The maturing Kamchatkan sockeye salmon were found eastward to a distance of 500–700 miles from their rivers of origin, whereas the immatures were found as much as 1100 or 1200 miles from their rivers of origin.

These great distances of migration have been observed even for the youngest age groups of both Bristol Bay and Kamchatkan sockeye salmon which have been taken on the high seas, namely those fish which have spent but a little more than 1 year in the ocean.

In addition to using *T. crassus* as an indicator of the qualitative ocean distribution of Bristol Bay sockeye salmon, a comparison of the incidence of *Triaenophorus* infection in high-seas samples of maturing sockeye salmon with that in samples of sockeye salmon returning to spawn in Bristol Bay streams in the same year has permitted estimating the relative proportions of Bristol Bay maturing sockeye salmon in high-seas samples and subsequently defining the oceanic areas dominated by maturing fish of these stocks.

HOMING

One of the well-recognized aspects of the life history of salmon, which is most marked in the sockeye salmon, is the tendency to return to spawn in their natal streams. The data on *Triaenophorus crassus* infection provide confirmatory evidence of this "homing" phenomenon. Although sockeye salmon harboring *T. crassus*, and consequently of western Alaskan origin, have been found over very broad ocean areas, none has been found in the many samples of adults examined from nonwestern Alaskan estuaries or inshore areas, in spite of the fact that during their ocean residence *Triaenophorus*-infected sockeye salmon have been found much closer to sockeye salmon-producing areas other than those in which they originated. Further, there are extreme differences in the incidence of *T. crassus* infection in smolts from the different Bristol Bay river systems, which are paralleled by similar differences in the incidence of infection in returning adults. Thus, there appears to be no straying, at least no appreciable amount, even between streams whose mouths are only a few miles apart.

ORIGIN OF SALMONIDAE

Up to now only current aspects of the biology of Pacific salmons, as reflected in their parasites, have been considered. In the introductory remarks I noted that parasites may also provide clues to past events.

Ichthyologists have often discussed the question of a freshwater versus a marine origin of salmonids. Although the theory of freshwater origin is now generally accepted (see Hoar, 1958), arguments in support of the marine origin of salmonids have been published as recently as 1950 (Shmidt, 1947, 1950).

It has already been pointed out by Soviet parasitologists (Mamaev *et al.*, 1959) that evidence from parasitology supports the theory of a freshwater origin of salmonids. The evidence is based on the general principle "that a given host or type of host will have a larger variety of parasites, *particularly parasites peculiar to it* [italics mine], in the region where it has lived the longest, usually its place of origin" (Manter, 1955).

The Salmonidae are hosts of a variety of freshwater parasites which are specific to them, many being endoparasitic helminths with life histories involving one or more intermediate hosts. A number of these have been found in Pacific salmon (e.g. *Crepidostomum farionis*, *Eubothrium salvelini*, *Metabronema salvelini*, and *Philomena oncorhynchi*, to name a few). On the other hand there are no marine endoparasites and only two marine species of ectoparasites (the gill

monogenean *Gyrodactyloides strelkowi* and the copepod *Lepeophtheirus salmonis*) found in Pacific salmon which are specifically salmonid parasites.

These facts indicate that the freshwater environment must be an older habitat of salmon than is the marine environment and that anadromy is a comparatively recent development in the life of the salmon.

CONCLUDING REMARKS

Using the Pacific salmons as examples, I have attempted to show some of the ways in which parasitological data can contribute to an understanding of the biology of fishes. Examples of similar and other applications of parasitological data from both marine and freshwater fishes may be found in the biological literature (e.g. see: Bychowsky, 1933; Kabata, 1963; Manter, 1963; Shulman, 1954; Sindermann, 1961; Svetovidov, 1961; Szidat, 1961; and Zschokke, 1933).

As more knowledge on the parasite fauna of fishes and about the parasites themselves is accumulated it should be possible to make more extensive use of this information as an aid in the solution of various biological problems concerning fish.

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Effort Metabolism of Lateral Muscles in Carp[1]

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ABSTRACT

Effort induced by direct electrical stimulation of the lateral musculature of the carp led to effects which differed from one muscular tissue to another. With moderate effort, in the white muscle the glycogen concentration decreased and the pyruvate concentration increased; in the red muscle, the glycogen and pyruvate concentration did not change, but the amount of lactate and the oxygen consumption increased. With exhausting effort, the white muscle showed a decrease of glycogen and pyruvate, a great increase of lactate, without any significant modification of oxygen consumption; in the red muscle, there was a slight decrease of glycogen, an enormous rise of lactate, and a slight decrease of oxygen consumption. The sole modification observed in the liver was the increase of the lactate content after stimulation. Hypoxic conditions induced a great increase of the lactate:pyruvate ratio in the liver and in the red muscle, but not in the white. The findings suggest that the red muscle is a "burning place" of catabolites produced in the white muscle.

INTRODUCTION

Muscular fatigue in fish, more specifically the metabolic changes occurring after a muscular effort, has been the subject of a large number of investigations, especially in the last 10 years. Still little is known on the phenomena and on the mechanisms involved.

Canadian research (Black, 1958; Black *et al.*, 1959, 1962; Parker *et al.*, 1959) demonstrated the large accumulation of lactic acid in the blood of salmonids after exertion. The alteration of the normal ratio between anaerobic and aerobic processes may thus be one of the major mechanisms of the disturbances provoked by severe exercise.

Pora *et al.* (1962) showed that some metabolic changes occurring in heavily exercised carp may be attributed to an alarm reaction from some central nervous phenomena, rather than to energy consumption. In this study, we have expanded our research on modifications of the tissue metabolism, provoking exertion (in some cases fatigue) through direct excitation of the muscles.

METHODS AND MATERIAL

The experiments were carried out on hatchery carp weighing 250–450 g, and kept in tanks with flowing water, without nutrition, at 8–14 C.

Excitation was made *in situ*, the fish being fixed on a cork plate in a water-filled container. Induction shocks, regulated with a contact metronome in the primary circuit of the inductor to give a frequency of one double shock

[1]Received for publication February 9, 1965.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

per second were used. A steel-needle electrode was introduced into the musculature of the tail peduncle at the level of the lateral line. The other electrode was a copper plate fixed on the tail region, heterolaterally to the first one. Muscle samples were taken from the tail peduncle near the lateral line and liver samples were taken in the region of the gall bladder.

Oxygen consumption by the white and red muscular tissue and by the liver tissue was determined. Glycogen, pyruvic acid, and lactic acid content of these tissues were also measured. The experiments were carried out with four treatments (including NORMAL fish).

STIMULATED. Stimulation began with a tension value a little above the threshold and was pursued till the contraction amplitude decreased to nearly zero; then the contractility was tested through a slight increase of the tension. Duration of the excitation was 10–20 min.

EXHAUSTED. Stimulation began as by the preceding series, but continued with increasing tensions, till no contraction was obtained. Duration of the excitation was 40–70 min.

CONTROL. These were maintained in the installation 1 hr but were not stimulated.

Oxygen consumption was determined in a Warburg apparatus, incubating the tissue slices in a bicarbonate-free Ringer solution, glucose added, at pH 7 and 21 C. Glycogen determinations were carried out by the method of Montgomery (1957). Pyruvic acid was determined by the method of Rindi and Ferari (1956), and lactic acid by the method of Barker and Summerson (1941). The tissue pieces for biochemical determinations were frozen at –70 C immediately after sampling (maximum 2–3 min).

RESULTS

OXYGEN CONSUMPTION

Oxygen consumption was determined on two groups of fish. The first group included normal and stimulated treatments, the second group included normal, exhausted, and control treatments. The two normal treatments gave similar results for the muscular tissues, the difference between the means being insignificant. The results for the liver were significantly different. Therefore the data of each experimental treatment must be compared with those of the corresponding normal treatment.

There was an evident increase of oxygen consumption in the red muscle, caused by the muscular work, but in the white muscle, the increase was not statistically significant (Table I). With exhaustion, the oxygen consumption of the muscles tended to decrease, but the differences were statistically significant in the red muscle only. The oxygen consumption of the liver was not changed.

GLYCOGEN CONCENTRATION

After stimulation but without exhaustion, glycogen content decreased in the white muscle, but not in the red muscle and in the liver (Table II). In the

TABLE I. Oxygen consumption expressed as μlitres O_2/min/g of dry tissue.

		White muscle	Red muscle	Liver
Normal I:	Mean	11.8	19.8	31.4
	Se[a]	±0.9	±1.2	±3.2
	No.[b]	7	8	9
Stimulated:	Mean	15.5	28.6	31.5
	Se	±1.9	±2.3	±4.0
	No.	8	8	9
	Difference[c]	+31	+44	–
	Probability[d]	>0.05	<0.01	–
Normal II:	Mean	9.7	18.7	22.4
	Se	±1.0	±1.7	±2.0
	No.	9	9	9
Control:	Mean	9.9	18.9	19.3
	Se	±1.0	±1.0	±1.4
	No.	9	9	9
	Difference	+2	+1	−14
	Probability	>0.05	>0.05	>0.05
Exhausted:	Mean	8.4	16.0	18.2
	Se	±0.8	±0.9	±0.6
	No.	8	8	7
	Difference	−15	−15	−6
	Probability	>0.05	≅0.05	>0.05

[a]Standard error.
[b]Number of individuals.
[c]Percentage difference from normal (in exhausted fishes, from the control values).
[d]Probability of this difference.

case of exhaustion, the glycogen reserve compared to normal was depleted in the two muscles, without any influence on the hepatic reserve. Compared to the control series, the decrease was not significant. Thus, the decrease must be attributed to the prolonged hypoxic conditions during the stimulation.

PYRUVIC ACID CONCENTRATION

The data (Table III) show that the stimulation caused an increase of the amount of the pyruvic acid in the white muscle; but in the red muscle and in

TABLE II. Glycogen concentration expressed as μg/mg of wet tissue.

		White muscle	Red muscle	Liver
Normal:	Mean	3.1	18.7	151
	Se[a]	±0.2	±0.9	±5
	No.[b]	21	22	20
Stimulated:	Mean	2.2	18.5	141
	Se	±0.3	±1.2	±5
	No.	14	15	14
	Difference[c]	−29	−1	−7
	Probability[d]	=0.02	>0.05	>0.05
Control:	Mean	2.3	17.0	138
	Se	±0.3	±0.5	±7
	No.	6	5	6
	Difference	−26	−9	−9
	Probability	>0.05	>0.05	>0.05
Exhausted:	Mean	2.0	15.7	146
	Se	±0.4	±0.5	±5
	No.	10	8	9
	Difference	−13	−8	+6
	Probability	>0.05	>0.05	>0.05

[a]Standard error.
[b]Number of individuals.
[c]Percentage difference from normal (in exhausted fishes, from the control values).
[d]Probability of this difference.

the liver, there was a tendency to decrease, although this was not statistically significant. The exhaustion caused an evident decrease of the content of pyruvic acid in the white muscle. In the red muscle and in the liver, there is also a decrease, but it appears, even more pronounced, in the controls too. Thus, in these two tissues, the decrease seems to be due to the experimental conditions. We mention also the similar behaviour of red muscle and of liver, clearly shown by the data of Table III.

LACTIC ACID CONCENTRATION

Concentrations of lactic acid in the same groups as glycogen and pyruvic acid determinations are given in Table IV.

TABLE III. Pyruvic acid concentrations expressed as mg/100 g of wet tissue.

		White muscle	Red muscle	Liver
Normal:	Mean	0.89	0.89	0.57
	Se[a]	±0.07	±0.11	±0.04
	No.[b]	15	16	13
Stimulated:	Mean	1.13	0.68	0.48
	Se	±0.08	±0.06	±0.03
	No.	15	15	15
	Difference[c]	+38	−24	−16
	Probability[d]	<0.05	>0.05	>0.05
Control:	Mean	1.00	0.29	0.21
	Se	±0.17	±0.03	±0.03
	No.	6	6	4
	Difference	+24	−67	−63
	Probability	>0.05	<0.01	<0.01
Exhausted:	Mean	0.55	0.38	0.25
	Se	±0.07	±0.05	±0.05
	No.	10	10	10
	Difference	−45	+31	+19
	Probability	≅0.01	>0.05	>0.05

[a]Standard error.
[b]Number of individuals.
[c]Percentage difference from normal (in exhausted fishes, from the control values).
[d]Probability of this difference.

Lactic acid determinations were repeated on a second group of normal and stimulated carp long after they entered the laboratory (Table V). Upon stimulation without exhaustion, the two groups differed only in the white muscle where long-starved fishes showed an increase of the lactic acid concentration.

Mean values of the ratio between the lactic and the pyruvic acid amount in the three studied tissues were calculated from the data in Tables III and IV and are presented in Table VI.

DISCUSSION

It seems that there is a paradox in our data. In white muscle only a moderate effort induced a decrease of the glycogen content[2] and here pyruvic

[2]This decrease is slight with respect to that observed by Black *et al.* (1962) for salmonids: 50–85%, depending on the degree and the duration of the effort.

TABLE IV. Lactic acid concentrations expressed as mg/100 g of wet tissue.

		White muscle	Red muscle	Liver
Normal:	Mean	165	81	14.4
	Se[a]	±1.1	±5.0	±1.3
	No.[b]	6	9	9
Stimulated:	Mean	167	115	23.0
	Se	±7.8	±12.1	±1.9
	No.	14	15	13
	Difference[c]	–	+41	+59
	Probability[d]	–	<0.05	<0.01
Control:	Mean	158	111	32.6
	Se	±14.9	±9.7	±3.4
	No.	5	6	5
	Difference	−4	+36	+126
	Probability	>0.05	<0.01	<0.01
Exhausted:	Mean	295	246	31.7
	Se	±12.4	±4.2	±1.2
	No.	10	8	8
	Difference	+87	+122	−3
	Probability	<0.01	<0.01	>0.05

[a]Standard error.
[b]Number of individuals.
[c]Percentage difference from normal (in exhausted fishes, from the control values).
[d]Probability of this difference.

acid accumulates. In the red muscle only the concentration of lactic acid increased (in the nonstarved fishes). The lactate:pyruvate ratio showed opposite variations in the two muscles and the oxygen consumption increased significantly in the red muscle only. Thus, it appears that anaerobic glycolysis is intensified by effort in the white muscle, and still we find here neither a greater amount of lactic acid, nor an increased oxygen consumption. We cannot explain this phenomenon otherwise, as supposing an elimination of the catabolites of the glycolysis (as pyruvic and/or lactic acid) from the white muscle. It is possible that this elimination takes place towards the liver, where the lactic acid concentration really increases; but extremely poor vascularization of the white muscle and the slight intensity of the general circulation by fish makes us assume that the elimination of the catabolites cannot take place only in this

TABLE V. Lactic acid concentrations in long-starved fishes, expressed as mg/100 g of wet tissue.

		White muscle	Red muscle	Liver
Normal:	Mean	129	104	25.5
	Se[a]	±9.4	±13.0	±2.3
	No.[b]	11	14	10
Stimulated:	Mean	180	145	44.6
	Se	±13.9	±7.3	±6.1
	No.	10	10	12
	Difference[c]	+40	+39	+75
	Probability[d]	<0.01	≦0.02	<0.02

[a]Standard error.
[b]Number of individuals.
[c]Percentage difference from normal.
[d]Probability of this difference.

TABLE VI. The lactate:pyruvate ratio.

		White muscle	Red muscle	Liver
Normal:	Ratio	183	90	25
Stimulated:	Ratio	148	169	48
	Difference[a]	−19	+88	+92
Control:	Ratio	158	383	155
	Difference	−14	+326	+520
Exhausted:	Ratio	536	647	127
	Difference	+239	+69	−18

[a]Percentage difference from normal (in exhausted fishes, from control).

way. On the other hand, the increase of the lactic acid in the red muscle and the rise of oxygen consumption in this tissue cannot be explained by a consumption of its own glycogen. Of course, the excess in lactic acid and in substrate for oxidation can come from other sources (lipids,[3] blood glucose). However, the findings suggest a transfer of the catabolites of the anaerobic glycolysis from the white muscle into the red one, where their oxidation might take place.

[3]According to Jonas and Bilinski (1964), the oxidation of lipids is more intensive in the red muscle than in the white one.

This concept is in good agreement with Breakkan's (1956) hypothesis, also maintained by us in previous papers (Pora and Wittenberger, 1960; Pora *et al.*, 1962; Wittenberger and Oros, 1961) with respect to the metabolic role of the lateral red muscle of fish.

With exhausting effort, under our experimental conditions, the observed modifications were due to the combination of two factors: the effort itself and the conditions of prolonged immobility and hypoxia (the fish lay in a limited quantity of water with one operculum immobilized through the fixation of the animal on the cork plate). Therefore, only the differences between the exhausted and the control fishes can be attributed to effort and fatigue.

The exhaustion induced no modification of the glycogen concentration of the white muscle, compared to the control animals, but the concentration of the pyruvic acid decreased,[4] the lactic acid concentration increased, and the oxygen consumption was not subjected to significant changes. It seems therefore, that a part of the catabolites comes from sources other than the glycogen reserve. It should be mentioned that all this occurred at a lowered glycogen level, the decrease being due at least partially to the experimental conditions. The great increase of the lactic acid concentration and of the lactate:pyruvate ratio (perhaps because of the great excess of hydrogen ions, caused by the hypoxia associated with a strong effort) shows a typical "oxygen debt" (Huckabee, 1958). However, the tissue under the conditions of the Warburg apparatus does not pay this debt.

Under the same conditions, similar modifications took place in the red muscle, but the lactic acid content increased still more than in the white muscle and the oxygen consumption *decreased*. It appears that here also an oxygen debt remains unpaid by the muscle.

In the liver, exhaustion induced no change in the parameters studied.

These data could be interpreted as follows:

The exhausting muscular effort induces, in the carp as in the higher vertebrates, an accumulation of lactic acid in the tissue, but in contrast with these, the excess of catabolites is not taken up by the liver, or at least not in the time that our experiments lasted.[5] Moreover, the excess of catabolites, which represents a stock of substance that must be oxidized, is not oxidized in the muscular tissues in which it is accumulated. It seems that the catabolite oxidizing capacity of the red muscle is surpassed and that there even takes place a perturbation of the oxidative metabolism, for, although the amount of substrate has increased, the oxygen consumption decreases. Thus, the oxygen debt remains unpaid at the level of the muscular tissues, and at that of the whole organism too, for a relatively long time. It is possible that this incapacity for regulating their aerobic metabolism to the extent of the necessities imposed by the anaerobic one, is the cause of the severe perturbations induced by a strong effort in fish, perturbations that can be lethal in species more sensitive

[4]This phenomenon has been observed also for salmonids (Black *et al.*, 1962).

[5]Black *et al.* (1962) have shown for salmonids a continuous increase of the lactacidaemia several hours long after the effort. It seems thus, that the transfer of the catabolites towards the liver is very slow in fish.

to hypoxia, as are the salmonids.[6] Our data would thus serve as new arguments in favour of the hypothesis expressed by many authors (Black, 1958; Black *et al.*, 1959; Parker *et al.*, 1959) that the death of fish after exercise is the effect of a state of hypoxia.

The modifications observed in the three tissues are given in Fig. 1.

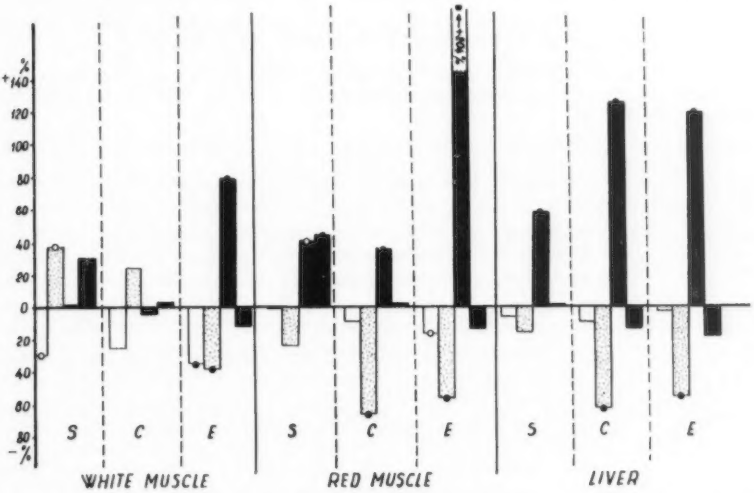

FIG. 1. Per cent modifications of the glycogen (white column), pyruvic acid (dotted column), and lactic acid (hatched column) content and of the oxygen consumption (black column). (All the values are related to those from the normal fishes. (S = stimulated; C = control; E = exhausted.) The columns with ● at the top indicate modifications significant at the 0.01 level, those with ○ at the 0.05 level.)

The great differences between the metabolism of the two muscular tissues, and also the metabolic resemblance of the red muscle and the liver, shown in previous papers (Pora and Wittenberger, 1960; Pora *et al.*, 1962; Wittenberger and Oros, 1961) become still more evident through the above data. Some of these differences seem to be general in vertebrates, the greater intensity of the glycolysis in the white muscles and that of the oxidative processes in the red muscles (Beatty *et al.*, 1963); other differences, as far as we know, have not yet been observed in other groups of animals.

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Bathymetric Distribution of Brittlestars (Ophiuroidea) Collected off the Northern Oregon Coast[1]

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ABSTRACT

A cooperative study by the Bureau of Commercial Fisheries and the U. S. Atomic Energy Commission was undertaken to evaluate the composition of benthic fauna indigenous to waters adjacent to the Columbia River mouth. Standard stations were established by 25-fath intervals between 50 and 500 fath, and by 50-fath intervals from 500 to 1050 fath. Fifty- to 500-fath stations were monitored seasonally while sampling of deeper stations was generally restricted to spring and summer cruises.

Twenty-four species of ophiuroids representing eight families and 14 genera were collected during this study. Species number varied by station ranging from one at 650 fath to a maximum of nine species at 300 fath.

The number of species of ophiuroids by benthic zone showed a general increase with increasing depth. The total number of species collected by benthic zone was 4 from the sublittoral, 8 from the upper bathyal, 13 from the lower bathyal, and 15 from the abyssal. One, three, and eight species were confined to the outer sublittoral, lower bathyal, and abyssal, respectively.

The highest availability of ophiuroids occurred between 150 and 250 fath and between 800 and 1050 fath. Lowest availability occurred at 125, 325, and 350 fath where few or no ophiuroids were observed. Larger catches of ophiuroids were estimated to contain from 500 to 2000 individuals. A single species, *Ophiura sarsii*, consistently dominated catches from 150 to 250 fath; while four species, *Ophiocten pacificum*, *Ophiolimna bairdi*, *Ophiomusium lymani*, and *Ophiophthalmus normani*, dominated catches between 800 and 1050 fath.

The families Ophiuridae and Ophiacanthidae predominate in the study area. Together, they account for the majority of species collected which include the five most abundant species.

The bathymetric distribution of ophiuroids from the Columbia River trackline illustrates a changing species composition with increasing depth, with the existence of both stenobathic and eurybathic species.

INTRODUCTION

In June 1961 the United States Bureau of Commercial Fisheries joined with the United States Atomic Energy Commission in a study of benthic fauna indigenous to the outer continental shelf and slope off the Columbia River mouth. Principal aims of this study were (1) to establish and systematically resurvey a set station plan for determining seasonal availability and bathymetric distribution of demersal fish and invertebrates, (2) to return a representative sample of the biota to the University of Washington Laboratory of Radiation Biology, for radiological analysis, to gain information on the biological transport of radionucleids originating in the Columbia River, and (3) to assemble information on deep-water latent marine resources. This report

[1]Received for publication April 23, 1965.

J. Fish. Res. Bd. Canada, 22(6), 1965.
Printed in Canada.

summarizes data on the bathymetric distribution of ophiuroids collected during A.E.C. cruises 1 through 14.

Among the major studies describing ophiurans of the Pacific are those by Lyman (1882) and Clark (1911). Lyman compiled an extensive monograph of the genera and species known up to 1881 with much of his source material collected by H. M. S. *Challenger* during explorations conducted from 1873 to 1876. Clark's 1911 report describes North Pacific ophiurans in the collection of the National Museum. Much of this source material was collected in 1900 and 1906, during explorations by the U. S. Fisheries steamer *Albatross*.

PHYSICAL FEATURES OF THE STUDY AREA

The study area is located southwest of the Columbia River mouth and lies almost parallel to the southern edge of Astoria Canyon (Fig. 1). This area lies within the subarctic Pacific region, the principal features of which are discussed by Dodimead *et al.* (1963) and Muromtsev (1958).

The unique hydrography existing in the study area is due primarily to seasonal changes in both the direction of prevailing winds and volume of Columbia River effluent entering the oceanic water. In winter, plume water — Columbia River effluent with a salinity less than 32.5‰ (Budinger *et al.*, 1964) — is successfully held against the coast by prevailing southerly winds; in spring,

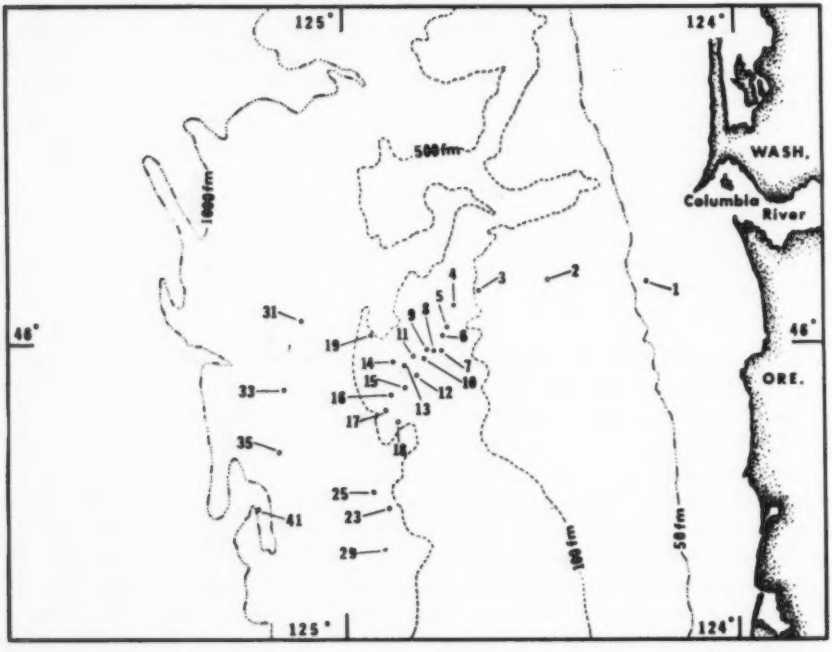

FIG. 1. Columbia River trackline showing approximate location of stations.

slackening winds plus increased Columbia River discharge result in a seaward flow; in summer, plume water is deflected to the southwest by prevailing northerly winds.

The pattern of surface temperatures along the trackline showed both a seasonal fluctuation and an offshore gradient. During cruise No. 7 (Table I) summer highs of 16.9 and 18.3 C were recorded from the 50- and 850-fath stations, respectively, while winter lows of 7.2 and 9.4 C were recorded during cruise No. 9 at the 50- and 1050-fath stations, respectively.

Temperature of water near bottom (Table II) decreased with increasing depth ranging from an approximated mean of 8.3 C at 50 fath to 2.3 C at 1000 fath. Bottom temperature variation, by station, was greatest at 50 fath where a high of 11.2 C (cruise No. 12) and a low of 6.8 C (cruise No. 14) showed a range of 4.4 C degrees. Progressively smaller differences occur with increasing depth with bottom temperatures below 100 fath fluctuating within 1 C degree. The 4 C isotherm occurred at approximately 475 fath.[2]

The salinity structure of the subarctic Pacific region includes a halocline defined by a salinity increase of 1‰ in the approximate depth interval of 55–109 fath; its lower limits can accurately be defined by an isohaline surface of

TABLE I. Dates of Bureau of Commercial Fisheries and Atomic Energy Commission cruises and vessels employed.

Cruise No.	Vessel	Date
1	*John N. Cobb*	June 4–16, 1961
2	*Commando*	June 24–July 12, 1961
3	*Commando*	September 9–22, 1961
4	*Commando*	November 27–December 13, 1961
5	*John N. Cobb*	February 23–March 19, 1962
6	*Commando*	May 14–June 13, 1962
7	*Commando*	August 21–September 9, 1962
8	*Commando*	October 25–November 7, 1962
9	*John N. Cobb*	January 21–February 6, 1963
10	*Commando*	April 29–May 17, 1963
11	*Commando*	August 19–September 5, 1963
12	*Commando*	October 28–November 14, 1963
13	*John N. Cobb*	January 8–22, 1964
14	*Commando*	May 12–June 5, 1964

[2]Unpublished data from a cruise of the Bureau of Commercial Fisheries vessel *George B. Kelez* (October 24–November 26, 1963).

TABLE II. Bottom temperature (*C*) and salinity (‰) collected from the Columbia River trackline.

Station No.	Depth (*fath*)		Cruise number									
			5	6	7	8	9	10	11	12	13	14
1A	50	T[a]	8.4	—	7.4	7.82	7.9	9.3	7.4	11.2	—	6.8
		S	33.651	—	33.86	—	33.78	33.06	—	—	—	—
2A	75	T	8.7	—	6.0	7.70	7.6	8.8	7.1	—	9.4	—
		S	33.411	—	33.96	—	33.84	33.71	—	—	—	33.616
3A	100	T	8.3	—	—	7.61	—	7.7	7.1	—	7.9	6.9
		S	33.825	—	—	—	33.20	33.88	—	—	—	33.673
4A	125	T	7.2	—	6.4	—	6.6	6.9	7.1	—	—	—
		S	33.972	—	33.99	—	33.90	33.98	34.030	—	—	—
5A	150	T	7.0	—	—	6.50	6.6	6.6	6.8	—	—	—
		S	33.977	—	—	—	33.98	33.81	34.050	—	—	—
6A	175	T	7.1	—	—	—	6.3	6.6	6.9	—	—	—
		S	33.953	—	—	—	34.01	33.99	34.007	—	—	—
7A	200	T	6.1	—	—	—	6.0	6.2	6.3	—	—	—
		S	34.002	—	34.08	—	—	33.87	34.057	—	—	—
8A	225	T	5.4	—	—	—	5.8	5.8	—	—	—	—
		S	34.010	—	—	—	—	34.04	—	—	—	—
9A	250	T	—	—	—	—	5.6	5.3	5.8	—	—	—
		S	—	—	34.08	—	34.05	34.12	34.099	—	—	—
10A	275	T	—	—	—	—	—	—	—	—	—	—
		S	—	—	—	—	—	34.05	—	—	—	—
11A	300	T	5.2	4.7	—	—	5.1	—	5.75	—	—	—
		S	34.061	—	—	—	34.06	—	—	—	—	—
13A	350	T	—	—	—	—	4.6	—	4.8	—	—	—
		S	—	—	—	—	34.18	—	34.216	—	—	—
14A	375	T	—	—	—	—	—	—	4.9	—	—	—
		S	—	—	—	—	—	—	—	—	—	—
15A	400	T	4.3	—	—	—	—	—	4.8	—	—	4.11
		S	34.236	—	—	—	—	—	34.270	—	—	—
16A	425	T	4.8	—	—	—	4.2	—	—	—	—	—
		S	34.137	—	—	—	34.27	—	—	—	—	—
17A	450	T	4.6	—	—	—	4.7	—	4.2	—	—	—
		S	34.192	—	—	—	34.13	34.31	34.327	—	—	—
19A	500	T	—	—	—	—	—	—	—	—	—	3.7
		S	—	—	—	—	—	—	—	—	—	—
23A	600	T	—	2.7	—	—	—	—	—	—	—	—
		S	—	—	—	—	—	—	—	—	—	—
25A	650	T	—	—	—	—	—	—	—	—	—	3.13
		S	—	—	—	—	—	—	34.436	—	—	34.424
29A	750	T	—	—	—	—	—	—	—	—	—	—
		S	—	—	—	—	—	—	34.472	—	—	—
31A	800	T	—	2.8	—	—	—	—	—	—	—	2.7
		S	—	—	—	—	—	—	—	—	—	34.495
33A	850	T	—	—	—	—	—	—	—	—	—	2.65
		S	—	—	—	—	—	—	—	—	—	34.445
35A	900	T	—	—	—	—	—	—	2.6	—	—	2.62
		S	—	—	—	—	—	—	34.557	—	—	34.472
39A	1000	T	—	—	—	—	2.3	—	—	—	—	—
		S	—	—	—	—	—	—	—	—	—	—

[a]T = temperature; S = salinity.

salinity equalling 33.8‰. In May 1963 the halocline was found at approximately 27–82 fath in waters adjacent to the Columbia River mouth (Ingraham, 1963). Salinity, near bottom, along the trackline increased with depth and varied from

a minimum of 33.06‰ (cruise No. 10) at 50 fath to a maximum of 34.557‰ at 900 fath.

The quantity of dissolved oxygen in water near bottom, declined from approximately 0.35 mg-at/liter at 50 fath (see footnote 2) to approximately 0.02 mg-at/liter at 475 fath (J. Ingraham, personal communication). Beyond this minimum, dissolved oxygen gradually increased to approximately 0.1 mg-at/liter at 900 fath.

Sediment analysis, from the Columbia River trackline, showed a general transition from silty-sand at 50–200 fath to sandy-silt at 250 fath to clay-silt at 300–400 fath to silty-clay at greater depths.

METHODS

The trackline begins approximately 10 miles SSW of the Columbia River mouth at the 50-fath contour and extends in a southwesterly direction to the 1050-fath contour. Standard stations were established by 25-fath intervals between 50 and 500 fath and by 50-fath intervals from 500 to 1050 fath (Table III). Standard stations 1A–19A (50–500 fath) were monitored seasonally while sampling of deeper stations was generally restricted to spring and summer cruises.

TABLE III. Approximate locations of standard sampling stations of the cooperative Bureau of Commercial Fisheries and Atomic Energy Commission marine investigations off the Columbia River mouth.

Station designation	Depth (*fath*)	N lat	W long	Station designation	Depth (*fath*)	N lat	W long
1A	50	46°07.8′	124°13.0′	14A	375	45°57.3′	124°50.5′
2A	75	46°04.8′	124°31.0′	15A	400	45°57.0′	124°53.3′
3A	100	46°04.1′	124°38.5′	16A	425	45°53.2′	124°47.2′
4A	125	46°01.8′	124°42.0′	17A	450	45°52.3′	124°52.1′
5A	150	46°00.8′	124°43.3′	18A	475	45°52.2′	124°52.2′
6A	175	46°00.0′	124°43.5′	19A	500	46°01.7′	124°55.2′
7A	200	45°59.8′	124°44.3′	23A	600	45°44.6′	124°53.8′
8A	225	45°58.2′	124°44.5′	25A	650	45°43.3′	124°54.8′
9A	250	45°59.3′	124°45.3′	29A	750	45°36.3′	124°53.7′
10A	275	45°57.2′	124°45.0′	31A	800	46°01.8′	125°04.5′
11A	300	45°58.5′	124°47.0′	33A	850	45°54.0′	125°08.8′
12A	325	45°56.5′	124°47.0′	35A	900	45°50.0′	125°10.6′
13A	350	45°57.3′	124°49.0′	41A	1050	45°42.2′	125°13.0′

The 93-ft Bureau of Commercial Fisheries vessel *John N. Cobb* (Ellson, 1952) conducted the initial and following winter explorations. The 65-ft M/V *Commando* was chartered from the University of Washington for spring, summer, and fall cruises. Both vessels were equipped with two winch drums each containing 1000 fath of ½-inch cable. Sampling to 1050 fath was accomplished by coupling both drums of cable in tandem using a purse seine swivel equipped with a standard ½-inch steel shackle.

A standard 400-mesh eastern otter trawl (Greenwood, 1958) with a 1½-inch mesh liner in the codend, for retention of smaller organisms, was used in sampling stations from 50 to 475 fath. Trawls used in sampling depths greater than 475 fath were (1) a 43-ft Gulf of Mexico flat shrimp trawl (Schaefers and Johnson, 1957) during cruises 6 and 7; and (2) a 70-ft semi-balloon shrimp trawl (Greenwood, 1959) during cruises 10, 11, and 14. Both shrimp trawls are constructed of 1½-inch mesh throughout and are drawn by a single tow cable.

Towing time, the interval between the setting of gear at the proper depth and the start of retrieve, varied from 30 min at 50- and 75-fath stations to 60 min at 100- to 450-fath stations to 38–90 min at depths greater than 450 fath. All trawls were towed during daylight hours at an approximate speed of 2.5 knots.

Preliminary results of gear comparison tests recently conducted between the 70-ft and 400-mesh trawls indicated that the catching efficiency, for ophiuroids only, approached 1:1. Since the effective width opening of the 43-ft trawl approximates one-half the opening of both the 70-ft and 400-mesh trawls, catches of the smaller gear were doubled to equate the catch-per-unit effort. All tows were then adjusted to 60 min, assuming that the catch-per-unit time was similar.

Infaunal samples were obtained by a Smith-McIntyre grab (Smith, 1954) during cruises 8, 10, and 11, and a Forster anchor dredge (Forster, 1953) during cruise 14. The 0.1 m^2 Smith-McIntyre quantitative grab was weighted with 100 lb of lead to facilitate both proper orientation with, and penetration of, bottom. Successful operation was limited to a maximum depth of 250 fath. The anchor dredge was operated successfully to 400 fath by fastening two dredges back to back when sampling stations deeper than 150 fath. It was assumed that this dual arrangement would increase the probability of obtaining a sample in the event the dredge should flip over during its descent.

Near-bottom water samples and temperatures were collected with a standard Nansen bottle equipped with a reversing thermometer. Salinities were determined with an inductive salinometer by the Bureau's Biological Laboratory in Seattle. Core samples, obtained with a 6-ft gravity corer, were analyzed for substrate composition by the University of Washington Department of Oceanography.

When possible, catches of ophiuroids were separated by species and individually counted or weighed on hand scales. Most often, time restrictions permitted only a cursory examination of the catch: total number was estimated visually, conspicuous forms were noted, and a representative sample was

retained for later identification. The returned samples were checked against previously identified material; all questionable forms and new species were sent to Mr Fred C. Ziesenhenne for identification.

Benthic zonation follows the classification of Hedgpeth (1957) and Bruun (1957). The outer sublittoral extends from the 50-fath station to the edge of the continental shelf at about 100 fath. The bathyal extends from the shelf edge to a point within the 475- to 500-fath depth interval where the 4 C isotherm intercepts the continental slope. The abyssal is confined to depths where temperatures are less than 4 C. The bathyal was separated into upper and lower zones to facilitate the presentation of data.

LIMITATION OF DATA

Factors which influenced the results of this study were: (1) variation in gear performance; (2) method of equating the catching efficiency between dissimilar trawls; (3) a disproportionate fishing effort between stations; (4) selectivity of sampling devices and trawling locations; and (5) the method of estimating catches of ophiuroids.

The variations in trawl performance and speed probably resulted in unequal coverage of bottom area per unit time with concomitant errors in the catch-per-unit effort.

The catching efficiency of the 43-ft shrimp trawl has not been correlated to the other trawls; therefore, the procedure of doubling the catch to equate these gears is based upon a subjective evaluation.

Fishing effort between stations ranged from 15 drags at 50 fath to 2 drags at 500, 650, 800, and 1050 fath. The data collected from more frequently sampled stations should more accurately represent both the species composition and availability of ophiuroids.

Sampling devices used were undoubtedly selective. For example, the frequency of occurrence of *Amphioplus strongyloplax* in bottom grab samples indicates a relatively high density and yet, none was observed in trawl catches. Also, the selection of trawling locations was dependent upon the suitability of bottom; rocky or rough areas, were avoided. Therefore, data on the availability of ophiuroids are probably biased by both the inherent selectivity of individual fishing gears and the repeated selection of specific trawling sites.

The number of ophiuroids, for most catches, was visually estimated *in toto*; therefore, abundance figures may be somewhat inaccurate. For determining species composition, a representative sample was selected by briefly examining the catch for specimens unique in size and form. Similarly appearing species may have been overlooked and would not then be included in the data.

RESULTS

Twenty-four species of ophiuroids representing eight families and 14 genera were collected during this study (Table IV). The number of species varied from nine in the family Ophiuridae to one in families Gorgonocephalidae, Asteroschematidae, and Ophiomyxidae. Families Ophiacanthidae, Amphiuridae,

TABLE IV. List of ophiuroids collected from the Columbia River trackline.

Class ASTEROZOA
Subclass OPHIUROIDEA
Order OPHIURIDA
Suborder EURYALAE
Family GORGONOCEPHALIDAE
Gorgonocephalus caryi
Family ASTERONYCHIDAE
Asteronyx excavata
Asteronyx loveni

Family ASTEROSCHEMATIDAE
Astroschema sp.

Suborder OPHIURAE
Family OPHIOMYXIDAE
Ophiocynodus corynetes

Family OPHIACANTHIDAE
Ophiacantha diplasia
Ophiolimna bairdi
Ophiophthalmus cataleimmoidus
Ophiophthalmus normani

Family AMPHIURIDAE
Amphioplus strongyloplax
Amphiodia euryaspis
Amphiura koreae

Family OPHIACTIDAE
Ophiopholis bakeri
Ophiopholis aculeata var. *kennerlyi*
Ophiopholis longispina

Family OPHIURIDAE
Ophiocten pacificum
Ophiomusium jolliensis
Ophiomusium lymani
Ophiomusium multispinum
Ophiura hadra
Ophiura irrorata
Ophiura ponderosa
Ophiura sarsii
Ophiura leptoctenia

Ophiactidae, and Asteronychidae were represented by 4, 3, 3, and 2 species, respectively.

NUMBER OF SPECIES BY BENTHIC ZONE

The number of species by benthic zone increased with depth, ranging from a low of four in the outer sublittoral to a high of 15 from the abyssal. The upper and lower bathyal were represented by eight and 13 species, respectively. A similar increase with depth occurred for both the gain and loss of species by benthic zone: Five, seven, and 10 species were gained in the upper bathyal, lower bathyal, and abyssal zone, respectively; while 1, 2, and 8 species were lost from the upper bathyal, lower bathyal, and abyssal zone, respectively (Table V).

TABLE V. Distribution of ophiuroids by benthic zone.

Benthic zone	Outer sublittoral	Upper bathyal	Lower bathyal	Abyssal
Depth range (*fath*)	50–100	125–275	300–450	500–1050
Temperature *C* (range)	11.2–6.9	7.2–5.3	5.75–4.2	3.7–2.3
Salinity ‰ (range)	33.06–33.88	33.90–34.05	34.06–34.327	34.360[a]–34.557
Bottom type	Silty sand	Silty sand to sandy silt	Clayey silt to silty clay	Silty clay
SPECIES				
Gorgonocephalus caryi	x			
Amphioplus strongyloplax	x	x	x	
Ophiopholis bakeri	x	x	x	
Ophiura sarsii	x	x	x	
Ophiura ponderosa		x	x	
Ophiophthalmus cataleimmoidus		x	x	
Ophiacantha diplasia		x		x
Amphiura koreae		x		x
Asteronyx loveni		x	x	x
Asteronyx excavata?			x	
Ophiopholis aculeata var. *kennerlyi*			x	
Amphiodia euryaspis			x	
Ophiocynodus corynetes			x	x
Ophiopholis longispina			x	x
Ophiomusium jolliensis			x	x
Ophiophthalmus normani			x	x
Ophiomusium lymani				x
Ophiolimna bairdi				x
Ophiocten pacificum				x
Ophiomusium multispinum				x
Ophiura leptoctenia				x
Ophiura hadra				x
Ophiura irrorata				x
Astroschema sp.				x
Species total	4	8	13	15
Species gained		5	7	10
Species lost		1	2	8

[a]From Ingraham (1963).

Of the 24 species identified, 12 were confined to a single benthic zone. One was confined to the outer sublittoral, three to the lower bathyal, and eight to the abyssal. Of the 12 species not confined within a benthic zone, three ranged from the outer sublittoral to the lower bathyal, two from the upper bathyal to the lower bathyal, four from the lower bathyal to abyssal, and three from the upper bathyal to abyssal.

General Abundance of Ophiuroids

The highest availability of ophiuroids (Table VI), in terms of rank abundance, occurred at two depth intervals: between 150 and 250 fath and between 800 and 1050 fath. The lowest availability occurred at 125, 325, and 350 fath where few or no ophiuroids were observed. The largest catches of ophiuroids were estimated to contain from 500 to 2000 individuals. Catches of this magnitude occurred at 150 fath (cruises 2 and 11), 175 fath (cruise 9), 200 fath (cruises 9, 11, and 14), 225 fath (cruise 7), 250 fath (cruises 4, 7, and 10), and at 900 and 1050 fath (cruise 14).

A single species, *Ophiura sarsii*, consistently dominated the catches in one of the two depth intervals showing the highest availability of ophiuroids (150–250 fath). Conversely, several species were dominant in catches collected from the other area of highest availability (800–1050 fath), namely, *Ophiocten pacificum*, *Ophiolimna bairdi*, *Ophiomusium lymani*, and *Ophiophthalmus normani* (Table VII).

Ophiuroids belonging to two of the eight families represented predominate in the study area. The families Ophiuridae and Ophiacanthidae account for 13 of the 24 species collected which include the five most abundant species.

During infaunal sampling, ophiuroids were collected from 10 of 16 grab samples between 50 and 250 fath and from 6 of 10 dredge tows between 50 and 450 fath. Only two species, *Ophiura sarsii* and *Amphioplus strongyloplax*, were collected with the quantitative grab. Density ranged from none to a maximum of 60 *A. strongyloplax*/m^2 at 125 fath and 30 *O. sarsii*/m^2 at 150 and 250 fath. Four species, *O. sarsii*, *A. strongyloplax*, *Amphiura koreae*, *and Ophiura ponderosa*, were collected with the anchor dredge.

Synopsis of the Species

Bathymetric Distribution, Availability, and General Geographic Distribution

Species are presented by family following the classification of Fell (1960). Bathymetric distribution and availability sections pertain exclusively to data collected in this study. The general geographic distribution section takes into account reports of others. Tables V, VI, and VII should be referred to regarding information on benthic zonation, number of drags by station, and the verbal description of rank abundance which will be followed in estimating the number of individuals when actual numbers are not available.

TABLE VI. Rank abundance for number of ophiuroids per 1-hr drag by stations for cruises 1–14 (June 1961 to May 1964).

Standard stations	Depth (*fath*)	Cruise number													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1A	50	–[a]	0[b]	0	0	0	2	0	0	2	0	0	0	0	1[b]
2A	75	–	1[b]	–	–	2	2	0	2	3	1	2	–	2	–
3A	100	–	1[b]	–	0	1	0	0	0	0	0	0	0	0	1
4A	125	–	0[b]	0	–	1	0	0	–	1	0	0	–	0	–
5A	150	–	5[b]	1	0	3	2	3	0	4	4	5	–	–	–
6A	175	–	4[b]	0	–	0	4	1	–	5	2	1	–	–	–
7A	200	–	4[b]	1	4	2	3	4	–	5	0	5	–	2	5
8A	225	–	4[b]	4	–	4	3	5	–	4	4	3	–	–	–
9A	250	–	1[b]	4	5	0	2	5	–	4	5	4	–	–	–
10A	275	–	0	0	0	–	0	0	–	–	4	2	–	–	–
11A	300	–	0	4	0	1	2	3	–	2	2	0	–	–	–
12A	325	–	1	0	1	0	1	0	–	1	1	1	–	–	–
13A	350	–	0	1	0	0	1	0	–	1	1	0	–	–	–
14A	375	–	0	0	1	0	0	3	–	0	2	0	–	–	–
15A	400	–	1	0	1	0	0	1	–	1	1	1	–	–	2
16A	425	2[b]	0	–	–	0	–	–	–	0	–	–	–	–	–
17A	450	–	1	–	0	1	1	1	–	1	2	0	–	–	–
19A	500	–	–	–	–	–	0	–	–	–	–	–	–	–	3
23A	600	–	–	0	–	–	3	1	–	–	–	–	–	–	1
25A	650	–	–	–	–	–	–	0	–	–	–	1	–	–	3
29A	750	–	–	–	–	–	0	0	–	–	2	1	–	–	0
31A	800	–	–	–	–	–	2	0	–	–	–	–	–	–	4
33A	850	–	–	–	–	–	4	0	–	–	4	4	–	–	4
35A	900	–	–	–	–	–	4[b]	4	–	–	–	2	–	–	5
41A	1050	–	–	–	–	–	2	–	–	–	–	–	–	–	5

RANK ABUNDANCE KEY

Rank no.	*Verbal description*	*Numerical description*
1	few	1–5
2	several	6–25
3	many	26–100
4	numerous	101–500
5	very numerous	500+

[a]Not fished.
[b]Two drags (averaged).

TABLE VII. Observed bathymetric distribution of ophiuroids collected from the Columbia River trackline.

Standard station	1A	2A	3A	4A	5A	6A	7A	8A	9A	10A	11A	12A	13A	14A	15A	16A	17A	19A	23A	25A	29A	31A	33A	35A	41A
Depth (*fath*)	50	75	100	125	150	175	200	225	250	275	300	325	350	375	400	425	450	500	600	650	750	800	850	900	1050
Total drags[a]	15	10	14	11	12	10	13	10	11	8	10	10	10	10	11	5	8	2	4	2	4	2	4	5	2
Percentage drags with ophiuroids	20.0	80.0	21.4	18.2	75.0	70.0	84.8	90.0	72.7	25.0	60.0	60.0	40.0	30.0	63.6	20.0	75.0	50.0	75.0	100	50.0	100	100	100	100
SPECIES																									
Gorgonocephalus caryi	x	x																							
Amphioplus strongyloplax[b]	x	x	x	x	x	x	x		x		x														
Ophiopholis bakeri		x			x	x	x			x				x											
Ophiura sarsii			x	x	x	x	x	x	x		x						x								
Asteronyx loveni					x		x				x	x		x			x				x	x	x		
Ophiacantha diplasia			-		x													x							
Ophiura ponderosa							x	x	x		x														
Amphiura koreae									x										x	x			x	x	x
Ophiophthalmus catateimmoidus									x		x														
Ophiopholis longispina											x							x							
Asteronyx excavata ?											x														
Ophiocynodus corynetes											x				x			x							
Ophiomusium jolliensis											x		x		x		x	x				x			
Amphiodia euryaspis												x													
Ophiophthalmus normani															x		x				x	x	x	x	x
Ophiopholis aculeata var. *kennerlyi*															x										
Ophiomusium lymani																					x	x	x	x	x
Ophiura hadra																					x	x	x	x	
Ophiura leptoctenia																							x		
Ophioilimna bairdi																							x	x	x
Ophiocten pacificum																							x	x	x
Ophiomusium multispinum																								x	x
Ophiura irrorata																								x	
Astroschema sp.																			x				x		
Asteronyx sp.[c]																									
Number of species	2	3	2	2	5	3	5	3	6	2	9	2	2	2	5		4	4	2	1	4	6	8	8	6
Ophiuroids[c]	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x		x				x		

[a]Refers to successful tows of 400-mesh commercial otter trawl, 43-ft Gulf of Mexico shrimp trawl, and 70-ft semi-ballon shrimp trawl.
[b]Specimens collected with a Smith-McIntyre quantitative grab or Forster anchor dredge only.
[c]Specimens not available for identification.

Family **GORGONOCEPHALIDAE** Ljungman, 1867
emend. Mortensen, 1933

Gorgonocephalus caryi Lyman, 1860

BATHYMETRIC DISTRIBUTION: Confined to outer sublittoral (50–75 fath).

AVAILABILITY: St. 1A; Cr. 9 (9):[3] St. 2A; Cr. 2, 6, 8, and 10 (few), Cr. 5 (10), Cr. 9 (13), Cr. 11 (10).

GEOGRAPHIC DISTRIBUTION: Japan, Aleutians, Bering Sea, Alaska, Washington, Oregon, and California, 8–576 fath (Clark, 1911).

Family **ASTERONYCHIDAE** Verrill, 1899
emend. Mortensen, 1933

Asteronyx excavata? Lutken and Mortensen, 1899

BATHYMETRIC DISTRIBUTION: Confined to lower bathyal (300 fath).

AVAILABILITY: St. 11A; Cr. 5 and 6 (1).

GEOGRAPHIC DISTRIBUTION: Mexico, 146–676 fath (Lutken and Mortensen, 1899); California, Oregon, 300–525 fath (Clark, 1913; trackline data).

Asteronyx loveni Muller and Troschel, 1842

BATHYMETRIC DISTRIBUTION: Discontinuous from upper bathyal to abyssal (150–850 fath).

AVAILABILITY: St. 5A; Cr. 2 (2): St. 7A; Cr. 2 (many): St. 11A; Cr. 6 and 9 (few): St. 12A; Cr. 2 and 4 (few): St. 14A; Cr. 4 (5): St. 17A; Cr. 2 and 5 (few), Cr. 9 (5): St. 29A; Cr. 10 (4): St. 31A; Cr. 6 (5), Cr. 14 (many): St. 33A; Cr. 6 (6), Cr. 14 (many).

GEOGRAPHIC DISTRIBUTION: Japan, Bering Sea, Alaska, Washington, Oregon, and California, 83–1620 fath (Clark, 1911; Diakonov, 1954; trackline data).

Family **ASTEROSCHEMATIDAE** Verrill, 1899
restr. Mortensen, 1933

Astroschema sp.

BATHYMETRIC DISTRIBUTION: Confined to abyssal (600 and 800 fath).

AVAILABILITY: St. 23A; Cr. 6 (few): St. 31A; Cr. 14 (several).

Family **OPHIOMYXIDAE** Ljungman, 1866

Ophiocynodus corynetes Clark, 1911

BATHYMETRIC DISTRIBUTION: Discontinuous from lower bathyal to abyssal (300–500 fath).

AVAILABILITY: St. 11A; Cr. 6 and 10 (few): St. 15A; Cr. 11 (1), Cr. 14 (+):[4] 19A; Cr. 14 (6).

GEOGRAPHIC DISTRIBUTION: California, 410–440 fath (Hartman and Barnard, 1958); Washington, Oregon, 300–685 fath (Clark, 1911; trackline data).

Family **OPHIACANTHIDAE** Perrier, 1891

Ophiolimna bairdi (Lyman), 1883

BATHYMETRIC DISTRIBUTION: Confined to abyssal (850–1050 fath).

AVAILABILITY: St. 33A; Cr. 11 (many), Cr. 14 (many): St. 35A; Cr. 6 and 7 (many), Cr. 11 (few), Cr. 14 (numerous): St. 41A; Cr. 14 (numerous).

GEOGRAPHIC DISTRIBUTION: North Circumpolar, 500–1400 fath (Fell, 1960).

Ophiophthalmus cataleimmoidus (Clark) 1911

BATHYMETRIC DISTRIBUTION: Confined to bathyal (250 and 300 fath).

AVAILABILITY: St. 9A; Cr. 11 (+): St. 11A; Cr. 3 (4).

GEOGRAPHIC DISTRIBUTION: North Pacific, 138–695 fath (Clark, 1911).

[3]St. = Station, Cr. = Cruise (number of individuals).

[4](+) species collected, numerical estimate not possible.

Specimens not available for identification.

Ophiacantha diplasia Clark, 1911

BATHYMETRIC DISTRIBUTION: Discontinuous from upper bathyal to abyssal (150 and 500 fath).

AVAILABILITY: St. 5A; Cr. 6 (few): St. 19A; Cr. 14 (5).

GEOGRAPHIC DISTRIBUTION: Oregon, California, 39–727 fath (Clark, 1911; Hartman and Barnard, 1958).

Ophiophthalmus normani (Lyman) 1879

BATHYMETRIC DISTRIBUTION: Discontinuous from lower bathyal to abyssal (400–1050 fath).

AVAILABILITY: St. 15A; Cr. 11 (+): St. 17A; Cr. 9 (1): St. 29A; Cr. 11 (1): St. 31A; Cr. 6 (8), Cr. 14 (many): St. 33A; Cr. 6 (many), Cr. 10 (numerous), Cr. 11 and 14 (many): St. 35A; Cr. 6 (several, 2 drags), Cr. 7 (few), Cr. 11 (8): St. 41A; Cr. 14 (several).

GEOGRAPHIC DISTRIBUTION: Japan, Oregon, Washington, and Alaska, 40–1050 fath (Clark, 1911; trackline data); Bering Sea, Kuril Islands, 55–1640 fath (Baranova, 1957; Diakonov, 1954); California, 620–957 fath (Hartman and Barnard, 1958, 1960).

Family **AMPHIURIDAE** Ljungman, 1867

Amphioplus strongyloplax Clark, 1911

BATHYMETRIC DISTRIBUTION: Discontinuous from sublittoral to lower bathyal (50–300 fath).

AVAILABILITY: Bottom grab samples only: St. 1A; Cr. 8 (3): St. 2A; Cr. 10 (3), Cr. 11 (3): St. 3A; Cr. 8 (4), Cr. 10 (1), Cr. 11 (1): St. 4A; Cr. 10 (7): St. 6A; Cr. 10 (2). Anchor dredge samples only: St. 2A; Cr. 14 (+): St. 3A; Cr. 14 (8): St. 5A; Cr. 14 (17): St. 7A; Cr. 14 (3): St. 9A; Cr. 14 (5): St. 11A; Cr. 14 (+).

GEOGRAPHIC DISTRIBUTION: Washington, 171 fath (Clark, 1911); California, Oregon, 25–300 fath (Barnard and Ziesenhenne, 1961; trackline data).

Amphiodia euryaspis Clark, 1911

BATHYMETRIC DISTRIBUTION: Confined to lower bathyal (325 fath).

AVAILABILITY: St. 12A; Cr. 6 (1).

GEOGRAPHIC DISTRIBUTION: Japan, Bering Sea, Oregon, and California, 68–325 fath (Clark, 1911; trackline data).

Amphiura koreae Duncan, 1879

BATHYMETRIC DISTRIBUTION: Discontinuous from upper bathyal to abyssal (250–1050 fath).

AVAILABILITY: St. 9A; Cr. 14 (3, anchor dredge): St. 23A; Cr. 7 (1), Cr. 14 (2): St. 25A; Cr. 11 (1), Cr. 14 (many): St. 33A; Cr. 11 (2): St. 35A; Cr. 6 (2), Cr. 14 (many): St. 41A; Cr. 14 (many).

GEOGRAPHIC DISTRIBUTION: California, 475–659 fath (Clark, 1913); Japan, 39–749 fath (Matsumoto, 1917); Panama, Ecuador, and Mexico, 511–1573 fath (Lutken and Mortensen, 1899); Oregon, 250–1050 fath (trackline data).

Family **OPHIACTIDAE** Matsumoto, 1915

Ophiopholis bakeri McClendon, 1909

BATHYMETRIC DISTRIBUTION: Discontinuous from sublittoral to lower bathyal (75–375 fath).

AVAILABILITY: St. 2A; Cr. 9 (1): St. 5A; Cr. 3 (2), Cr. 6 (few), Cr. 10 (+): St. 6A; Cr. 10 (4): St. 7A; Cr. 2 (+), Cr. 4 (+), Cr. 13 (few): St. 10A; Cr. 10 (+), Cr. 11 (9): St. 14A; Cr. 10 (6).

GEOGRAPHIC DISTRIBUTION: British Columbia, Washington, Oregon, and California, 41–375 fath (Clark, 1911; trackline data).

Ophiopholis aculeata var. *kennerlyi* Lyman, 1860

BATHYMETRIC DISTRIBUTION: Confined to lower bathyal (400 fath).

AVAILABILITY: St. 15A; Cr. 4 (4).

GEOGRAPHIC DISTRIBUTION: Bering Sea, Alaska, Washington, Oregon, and California, 16–400 fath (Clark, 1911; trackline data).

Ophiopholis longispina Clark, 1911

BATHYMETRIC DISTRIBUTION: Discontinuous from lower bathyal to abyssal (300 and 500 fath).

AVAILABILITY: St. 11A; Cr. 3 (+): St. 19A; Cr. 14 (8).

GEOGRAPHIC DISTRIBUTION: Oregon, Washington, and California, 277–685 fath (Clark, 1911).

Family **OPHIURIDAE** Lyman, 1865
(Syn. **OPHIOLEPIDIDAE** auctt.)

Ophiocten pacificum Lutken and Mortensen, 1899

BATHYMETRIC DISTRIBUTION: Confined to abyssal (850–1050 fath).

AVAILABILITY: St. 33A; Cr. 11 (3), Cr. 14 (many): St. 35A; Cr. 6 (19), Cr. 7 (8), Cr. 14 (numerous): St. 41A; Cr. 14 (numerous).

GEOGRAPHIC DISTRIBUTION: Washington, Japan, 501–876 fath (Clark, 1911); California, Oregon, 451–1090 fath (Clark, 1913; trackline data); Panama, Ecuador, Columbia, and Galapagos Islands, 770–1573 fath (Lutken and Mortensen, 1899).

Ophiomusium jolliensis McClendon, 1909

BATHYMETRIC DISTRIBUTION: Discontinuous from lower bathyal to abyssal (300–800 fath).

AVAILABILITY: St. 11A; Cr. 10 (1): St. 13A; Cr. 6 (few), Cr. 9 (1), Cr. 10 (few): St. 15A; Cr. 2 (1), Cr. 9 (2), Cr. 14 (several): St. 17A; Cr. 6 (1), Cr. 9 (+), Cr. 10 (1): St. 19A; Cr. 14 (few): St. 31A; Cr. 14 (+).

GEOGRAPHIC DISTRIBUTION: California, Oregon, Washington, and Japan, 75–800 fath (Clark, 1911; trackline data).

Ophiomusium lymani Thomson, 1873

BATHYMETRIC DISTRIBUTION: Confined to abyssal (750–1050 fath).

AVAILABILITY: St. 29A; Cr. 10 (1): St. 31A; Cr. 14 (+): St. 33A; Cr. 10 (+), Cr. 11 (14), Cr. 14 (many): St. 35A; Cr. 6 (48), Cr. 6 (+), Cr. 7 (many), Cr. 11 (7), Cr. 14 (numerous): St. 41A; Cr. 6 (3), Cr. 14 (many).

GEOGRAPHIC DISTRIBUTION: North Pacific and Northwestern Atlantic, 94–1588 fath (Clark, 1911, 1915).

Ophiomusium multispinum Clark, 1911

BATHYMETRIC DISTRIBUTION: Confined to abyssal (900 and 1050 fath).

AVAILABILITY: St. 35A; Cr. 6 (10), Cr. 7 (many), Cr. 11 (2), Cr. 14 (many): St. 41A; Cr. 6 (2), Cr. 14 (many).

GEOGRAPHIC DISTRIBUTION: California, Oregon, and Washington, 480–1760 fath (Clark, 1911, 1913; trackline data).

Ophiura hadra Clark, 1911

BATHYMETRIC DISTRIBUTION: Confined to abyssal (750–900 fath).

AVAILABILITY: St. 29A; Cr. 11 (1): St. 31A; Cr. 6 (1), Cr. 14 (few): St. 33A; Cr. 10 (+), Cr. 11 (1), Cr. 14 (few): St. 35A; Cr. 6 (+), Cr. 7 (1), Cr. 14 (+).

GEOGRAPHIC DISTRIBUTION: California, Oregon, and Washington, 451–930 fath (Clark, 1911, 1915; trackline data).

Ophiura irrorata (Lyman) 1878

BATHYMETRIC DISTRIBUTION: Confined to abyssal (900 fath).

AVAILABILITY: St. 35A; Cr. 6 (+), Cr. 7 (many).

GEOGRAPHIC DISTRIBUTION: Eastern Tropical Pacific, 1067–2232 fath (Lutken and Mortensen, 1899); North Pacific and North Atlantic, 470–1800 fath (Clark, 1911, 1915).

Ophiura ponderosa (Lyman) 1878

BATHYMETRIC DISTRIBUTION: Discontinuous, confined to bathyal (200–300 fath).

AVAILABILITY: St. 7A; Cr. 2 (+), Cr. 14 (+): St. 8A; Cr. 11 (+): St. 9A; Cr. 9 (+), Cr. 11 (+), Cr. 14 (1, anchor dredge); St. 11A; Cr. 9 (6).

GEOGRAPHIC DISTRIBUTION: Japan, California, Oregon, and Alaska, 75–505 fath (Clark, 1911; trackline data).

Ophiura sarsii Lutken, 1855

BATHYMETRIC DISTRIBUTION: Discontinuous from sublittoral to lower bathyal (100–450 fath).

AVAILABILITY: St. 3A; Cr. 11 (1, grab sample): St. 4A; Cr. 9 (few): St. 5A; Cr. 2 (very numerous), Cr. 6 (few), Cr. 9 (numerous), Cr. 10 (numerous, trawl; 3, grab sample): St. 6A; Cr. 2 (numerous), Cr. 2 (+), Cr. 9 (numerous), Cr. 10 (+, trawl; 1, grab sample): St. 7A; Cr. 2 (+), Cr. 3 (2), Cr. 4 (numerous), Cr. 5 (10), Cr. 9 (numerous), Cr. 13 (few), Cr. 14 (very numerous, trawl; 1, anchor dredge): St. 8A; Cr. 2 (+), Cr. 3 (numerous), Cr. 5 (numerous), Cr. 9 (numerous), Cr. 10 (1, grab sample), Cr. 11 (+): St. 9A; Cr. 3 (many), Cr. 4 (very numerous), Cr. 9 (numerous), Cr. 10 (very numerous, trawl; 3, grab sample), Cr. 14 (11, anchor dredge): St. 11A; Cr. 3 (numerous), Cr. 10 (+): St. 17A; Cr. 10 (few).

GEOGRAPHIC DISTRIBUTION: North Circumpolar, 5–695 fath (Clark, 1911, 1915).

Ophiura leptoctenia Clark, 1911

BATHYMETRIC DISTRIBUTION: Confined to abyssal (850 fath).

AVAILABILITY: St. 33A; Cr. 11 (1).

GEOGRAPHIC DISTRIBUTION: North Pacific, 67–1771 fath (Clark, 1911).

GENERAL REMARKS

Both the number of species and the species composition change with increasing depth (Table VII). The number of species by station ranged from 1 at 650 fath to a high of 9 at 300 fath. Deep-water stations, 800–1050 fath, maintained a relatively uniform, high number of species.

Considerable variation occurred in the bathymetric range shown by species. *Asteronyx excavata*, *Amphiodia euryaspis*, *Ophiopholis aculeata* var. *kennerlyi*, *Ophiura leptoctenia*, and *Ophiura irrorata* were each collected from a single depth, while the following species exhibited eurybathic characteristics: *Ophiophthalmus normani*, a 650-fath range; *Asteronyx loveni*, a 700-fath range; and *Amphiura koreae*, an 800-fath range.

The relatively large number of species frequently occurring from 800 to 1050 fath indicates that many of them probably extend into deeper water. The changing species composition along the trackline shows new species regularly appearing as depth increases, which leads one to speculate on the rich variety of forms that conceivably inhabit waters just beyond our deep-water stations.

Three species of ophiuroids were found associated with other organisms. *Gorgonocephalus caryi* and *Asteronyx loveni* were found epizoic with pennatulids. Both these species consistently appeared entwined about the sea pens rachis. Hyman (1955) stated that *A. loveni* may feed upon the pennatulids polyps as well as planktonic organisms. A few attached specimens of *Asteronyx loveni* were collected from 300 (cruise 9), 325 (cruise 10), and 450 fath (cruise 2 and 9), and many attached specimens were collected from 800 and 850 fath during

cruise 14. Similarly, a fan-shaped gorgonian of the genus *Callogorgia* was found harboring specimens of *Astroschema*. About 20 attached specimens of *Astroschema* were collected from 800 fath during cruise 14.

Mr Fred C. Ziesenhenne mentioned that specimens he identified as *Asteronyx excavata* showed some features of *Asteronyx loveni* variant, therefore the species should be considered with some reservation.

ACKNOWLEDGMENTS

The authors wish to extend special thanks to Mr Fred C. Ziesenhenne of the Allan Hancock Foundation, who promptly identified all the ophiurans presented in this report; Messrs Felix Favorite and James W. Ingraham, Jr., of the Bureau of Commercial Fisheries Biological Laboratory, Seattle, for unpublished oceanographic data collected off the Columbia River mouth; Drs Joseph Creager and Dean McManus of the University of Washington Department of Oceanography for their analysis of core samples; and to Dr Frederick Bayer of the University of Miami Institute of Marine Science for his identification of the gorgonian *Callogorgia*.

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A Survey of the Distribution of Intertidal Algae Along a Coast Transitional in Respect to Salinity and Tidal Factors[1,2]

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ABSTRACT

The dominant intertidal organisms studied in this survey were mostly brown, red, and green algae, together with a few species of marine flowering plants, barnacles, and molluscs. The flora of the northern shores of Juan de Fuca Strait show a transition between the flora of the open coast around Port Renfrew in the west, and that of the semi-sheltered coast near Victoria in the east.

The differences between the flora of Port Renfrew and that of Victoria can be studied as boundaries; the eastern boundaries of species occurring at Port Renfrew but not at Victoria, and the western boundaries of species occurring at Victoria but not at Port Renfrew. Fourteen eastern (inner) boundaries of open coast organisms, and four western (outer) boundaries of sheltered coast forms were found to be concentrated in the vicinities of Port Renfrew, Victoria, and Sooke, half way between.

Along Juan de Fuca Strait, Port Renfrew is the easternmost locality with a completely open coast environment, characterized by a salinity usually above 32‰. Sooke is the easternmost locality where water of 32‰ is found with some degree of frequency, probably as a result of upwelling associated with strong westerly winds. Victoria is the outermost locality where water of appreciably less than 30‰ may occur, because of heavy runoff from the Fraser River.

The author studied the vertical distributions of organisms by measuring upper and lower limits at 34 stations along the coast, plotting the heights obtained, and calculating regression lines for the points plotted. These limits were of four types: A. very variable along the whole coast; B. more variable between Port Renfrew and Sooke than between Sooke and Victoria; C. slightly variable, with a slope down from Port Renfrew to Victoria; and D. slightly variable, with little or no slope.

The slightly variable limits (C and D above) were used as a test of the theory that tidal factors can be used to explain, or at least describe, the vertical limits of intertidal organisms. The coast between Port Renfrew and Victoria shows a transition between a mixed semi-diurnal tide in the west and a diurnal tide in the east. Thus, the heights of the various tidal factors are usually different at Port Renfrew, Sooke, and Victoria, because of the different nature of the tides. The heights of most limits failed to correspond to the same tidal factor at these three places. The different patterns of variation and slope, found in the limits generally, indicate that it is unlikely that any other theory can provide a simple explanation of the height of most intertidal limits.

INTRODUCTION

The organisms selected for study comprise most of those dominating the intertidal zone in British Columbia. The many kelps of the order Laminariales

[1]Received for publication November 25, 1964.

[2]Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in the Department of Biology and Botany, University of B. C.

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J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

and other brown algae are the most conspicuous, while a number of smaller red and green benthonic algae, flowering plants, barnacles, and molluscs are sufficiently numerous to have been included (Table I).

The northern shore of Juan de Fuca Strait, on the southwest coast of Vancouver Island, is an exceptionally suitable environment for a study of the vertical and geographical distributions of these organisms. The shoreline is relatively straight and accessible, with a gradual transition from an open coastal environment at Port Renfrew, to a semi-sheltered one at Victoria. (A study of the physical oceanography of Juan de Fuca Strait has recently been made by Herlinveaux and Tully (1961).)

This transition from an open to a sheltered coast was described as far as possible in terms of the vertical and geographical distributions of individual species, and these distributions were correlated to factors in the environment.

In addition, this coast shows a transition from mixed semi-diurnal tides at Port Renfrew to diurnal tides at Victoria. There are such marked differences in tidal amplitude and period along this coast that almost any possible feature of the tidal curve must also vary in height. Measuring the height of both tidal features and the vertical limits of organisms at a number of points should provide a test for the theory (Doty, 1946) that tidal factors may be specifically related to vertical limits. If this theory is correct, the changes in height of the former along the coast should be reflected by similar changes in the latter.

METHODS

Observations were made at 34 stations along the coast (Fig. 1). These stations were chosen as representative of each major point and intervening bay. In the case of some of the most conspicuous algae, such as *Lessoniopsis* and *Macrocystis*, much of the coastline between stations was also investigated. Sea temperature was measured and salinity samples were taken, whenever a station was visited.

Heights in an intertidal survey are customarily determined by means of an Abney level and a measuring pole (Scagel, 1961). This method requires the services of two workers. Since the present study was for the most part conducted alone, a new method was developed which was more convenient for one person to use (Fig. 2). A pole was set up with a single, very obvious mark situated about 6 ft above low water level. A line was sighted from the horizon to the mark, and a plumb at the end of a measuring tape dropped from eye level to the object studied. The level of this object was then noted in the form of a negative value to be added to the height of the mark. The height of the mark, relative to a datum, was determined in the same way as the height of zero on the measuring pole is determined by the customary method. In this study, the height of the mark was determined by measuring the height of the sea at low tide, and assuming that the actual height of low water is the same as the predicted height.

The modified method had a number of additional convenient features. The pole need not be held upright. Obstructions in the line of sight between

TABLE I. List of organisms studied.

No.	Organism	Page reference to authority used in identification	Geographical distribution[c]	Vertical distribution[d]
	Green algae			
1.	Order Ulotrichales[a]		General[c]	Fig. 11
1a.	*Monostroma fuscum* var. *blytii* (Areschoug) Collins	Scagel, 1957, p. 34	Included in No. 1	Included in No. 1
1b.	*Enteromorpha linza* (Linnaeus) J. Agardh	Scagel, 1957, p. 41	"	"
1c.	*E. angusta* (Setchell and Gardner) Doty[b]	Doty, 1947a, p. 20	"	"
1d.	*E. vexata* (Setchell and Gardner) Doty[b]	Doty, 1947a, p. 21	Mostly epiphytic on *Egregia*	"
1e.	*Ulva lactuca* Linnaeus	Scagel, 1957, p. 44	Included in No. 1	"
1f.	*U. taeniata* (Setchell) Setchell and Gardner[b]	Doty, 1947a, p. 8	"	"
1g.	*U. lobata* (Kuetzing) Setchell and Gardner[b]	Doty, 1947a, p. 10	"	"
2.	Family Prasiolaceae[a]		General[c]	Fig. 11
2a.	*Prasiola meridionalis* Setchell and Gardner	Scagel, 1957, p. 47	Included in No. 2	Included in No. 2
2b.	*Rosenvingiella constricta* (Setchell and Gardner) Silva	"	"	"
3.	*Spongomorpha* spp.[a]		Fairly general[c]	Fig. 11
3a.	*S. coalita* (Ruprecht) Collins	Scagel, 1957, p. 57	Included in No. 3	Included in No. 3
3b.	*S. mertensii* (Ruprecht) Setchell and Gardner	Scagel, 1957, p. 57	Included in No. 3	Included in No. 3
3c.	*S. spinescens* Kuetzing	Scagel, 1957, p. 58	"	"
4.	*Codium fragile* (Suringar) Hariot	Scagel, 1957, p. 64	General[c]	Fig. 11
5.	*C. setchellii* Gardner	Scagel, 1957, p. 65	Fairly general[c]	"
	Brown algae			
6.	*Leathesia difformis* (Linnaeus) Areschoug	Scagel, 1957, p. 77	General[c]	"
7.	*Heterochordaria abietina* (Ruprecht) Setchell and Gardner	Scagel, 1957, p. 80	Fairly general[c]	"
8.	*Desmarestia intermedia* Postels and Ruprecht	Scagel, 1957, p. 82	General[c]	"
9.	*D. munda* Setchell and Gardner	Scagel, 1957, p. 84	Fairly general[c]	"

(*Continued*)

TABLE I. List of organisms studied. — (*continued*)

10.	*Laminaria* spp.[a]	Wilce, 1959	General[c]	"
10a.	*L. setchellii* Silva	Scagel, 1957, p. 97	Fig. 9	Included in No. 10
11.	*Pleurophycus gardneri* Setchell and Saunders, *In* Saunders	Scagel, 1957, p. 99	Fairly general[c]	Fig. 11
12.	*Cymathere triplicata* (Postels and Ruprecht) J. Agardh	Scagel, 1957, p. 99	"	"
13.	*Costaria* spp.[a]		General[c]	Fig. 11
13a.	*C. costata* (Turner) Saunders	Scagel, 1957, p. 100	Included in No. 13	Included in No. 13
13b.	*C. mertensii* J. Agardh	Scagel, 1957, p. 101	"	"
14.	*Hedophyllum sessile* (C. Agardh) Setchell, *In* Collins, Holden, and Setchell	Widdowson, 1965	Fig. 9	Fig. 11
15.	*Dictyoneurum californicum* Ruprecht	Scagel, 1957, p. 104	Fig. 9	UL:1.6 ft[d]
16.	*Nereocystis luetkeana* (Mertens) Postels and Ruprecht	"	General[c]	Fig. 11
17.	*Postelsia palmaeformis* Ruprecht	Scagel, 1957, p. 105	Fig. 9	UL:8.9 ft, LL:5.6 ft[d]
18.	*Macrocystis integrifolia* Bory	Scagel, 1957, p. 106	"	UL:0.4 ft[d]
19.	*Lessoniopsis littoralis* (Farlow and Setchell) Reinke	Scagel, 1957, p. 107	"	Fig. 11
20.	*Alaria marginata* Postels and Ruprecht	Widdowson, 1964, p. 59	Fig. 10	"
21.	*A. nana* Schrader	Widdowson, 1964, p. 62	Fig. 9	"
22.	*A. tenuifolia* Setchell, *In* Collins, Holden, and Setchell	Widdowson, 1964, p. 71	Fig. 10	"
23.	*Egregia menziesii* (Turner) Areschoug	Scagel, 1957, p. 111	Fig 9	"
24.	*Fucus distichus* Linnaeus	Powell, 1957	General[c]	"
24a.	*F. evanescens* C. Agardh	Scagel, 1957, p. 114	Included in No. 24	Included in No. 24
24b.	*F. gardneri* Silva	Scagel, 1957, p. 116	"	"
25.	*Pelvetiopsis limitata* (Setchell) Gardner	Scagel, 1957, p. 122	Fig. 9	UL:9.8 ft, LL:8.0 ft[d]
26.	*Cystoseira geminata* C. Agardh	"	Fig. 10	UL:0.4–1.2 ft[d]
27.	*Sargassum muticum* (Yendo) Fensholt	Scagel, 1957, p. 123	Fig. 10	UL:0.8–1.6 ft[d]
		Red algae		
28.	*Porphyra perforata* J. Agardh	Scagel, 1957, p. 130	General[c]	Fig. 11
29.	*P. schizophylla* Hollenberg[b]	Doty, 1947b, p. 161	Fairly general[c]	"

(*Continued*)

TABLE I. List of organisms studied. — (*Concluded*)

No.	Organism	Page reference to authority used in identification	Geographical distribution[c]	Vertical distribution[d]
30.	*Endocladia muricata* (Harvey) J. Agardh	Scagel, 1957, p. 160	Fairly general[c]	Fig. 11
31.	*Gigartina* spp.[a]		"	"
31a.	*G. agardhii* Setchell and Gardner[b]	Smith, 1944, p. 284	Included in No. 31	Included in No. 31
31b.	*G. cristata* (Setchell) Setchell and Gardner	Scagel, 1957, p. 185	"	"
31c.	*G. mamillosa* (Goodenough and Woodward) J. Agardh	Scagel, 1957, p. 187	"	"
31d.	*G. papillata* (C. Agardh) J. Agardh, *In* C. Agardh	Scagel, 1957, p. 188	"	"
32.	*Iridaea heterocarpa* Postels and Ruprecht	Scagel, 1957, p. 191	General[c]	Fig. 11
33.	*Halosaccion glandiforme* (Gmelin) Ruprecht	Scagel, 1957, p. 194	Fairly general[c]	"
34.	*Callithamnion pikeanum* Harvey	Scagel, 1957, p. 208	"	"
35.	*Rhodomela larix* (Turner) C. Agardh	Scagel, 1957, p. 241	General[c]	"
36.	*Odonthalia floccosa* (Esper) Falkenberg	Scagel, 1957, p. 242	"	"
	Marine flowering plants			
37.	*Phyllospadix scouleri* Hooker	Jepson, 1951, p. 67	Fig. 10	Fig. 11
38.	*Zostera marina* Linnaeus	Jepson, 1951, p. 66	"	UL:1.0 ft[d]
	Molluscs			
39.	*Mytilus californianus* Conrad	Johnson and Snook, 1927, p. 427	Fig. 10	Fig. 11
40.	*M. edulis* Linnaeus	Johnson and Snook, 1927, p. 428	"	UL:5.4 ft, LL:3.8 ft[d]
	Barnacles			
41.	*Chthamalus dallii* Pilsbry	Cornwall, 1955, p. 36	General[c]	Fig. 11
42.	*Mitella polymeris* Sowerby	Cornwall, 1955, p. 40	Fig. 9	"

[a]Problems in identification discussed in the text (p. 1432-1433).
[b]New records from British Columbia.
[c]"General" means widespread in British Columbia, including the Strait of Georgia; "fairly general" means widespread but not present in the Strait of Georgia.
[d]UL = upper limit; LL = lower limit.

FIG. 1. The topography of Juan de Fuca Strait and adjacent areas, showing sampling stations.

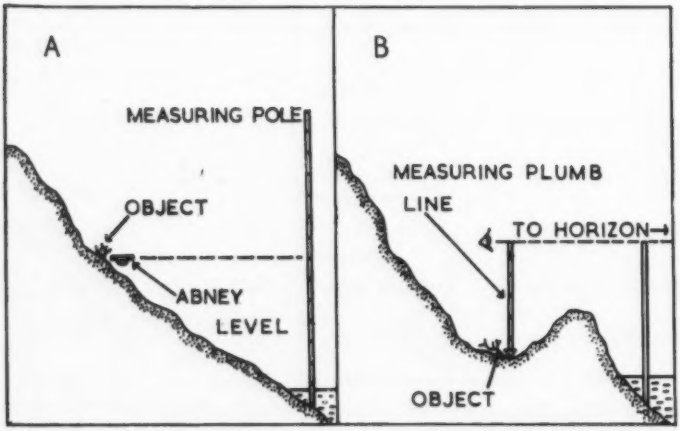

FIG. 2. Methods of determining heights in the intertidal zone (A. Usual method (Scagel, 1961); B. Method used in this survey).

the object to be levelled and the pole were not a difficulty, if they did not rise to the height of the mark on the pole. For night work the mark could be replaced by a light or, for repeated observations, by a permanent object, such as the top of a boulder. The levels of points some distance away from the pole could be determined, since only a mark had to be distinguished on it. On the other hand, the horizon had to be clear, and the study of objects above the mark required the use of another pole.

There are many sources of error in levelling. There is often much uncertainty in determining the vertical limits, even of such stable features as zones of large benthonic algae or sessile invertebrates. While a clearly defined upper limit is usually found, there may be "stragglers" above it. These stragglers are common in anomalous conditions, such as tide pools and under overhanging rocks. Lower limits are often indistinct. They may also be spurious, with the organism occurring unnoticed in the subtidal zone. This study is largely restricted to average upper limits, lower limits being noted only when they seemed distinct. The upper limits were average in the sense that they were taken as the highest point of common occurrence of the organism on relatively uniform rock, facing directly towards the sea. At certain locations levels were determined three times in the summer of 1957 and once again in the summer of 1958. When different values were obtained at different times, the mean value was used.

In addition, there are errors involved in rounding off the figures obtained, and from variation between the predicted and actual level of low water. The values obtained when the same limit was measured at different times for the same location were used to estimate the total error in the determination of levels. Using the values for 30 limits, each measured at three different times in the summer of 1957, standard deviation was found to be 0.7 ft. When using the values for 30 limits, each measured both in 1957 and 1958, it was found to be 0.4 ft. These are maximum values, since any actual changes in the height of a limit would appear as an error in these calculations.

Errors in the determination of geographical distributions are more difficult to estimate. An observation of the presence or absence of an organism at a locality is more reliable if the organism is very large, such as *Macrocystis*, or very frequent where it does occur, such as *Endocladia*.

Scagel's key (1957) was used for the identification of the algae. Where further information was needed, reference was made to the work of Smith (1944) on the Monterey Peninsula, and of Doty (1947a, b) in Oregon.

Johnson and Snook (1927) and Cornwall (1955) were the main general authorities used to identify the intertidal fauna and the barnacles in British Columbia. Marine flowering plants were identified from Jepson (1951).

In most cases, the conspicuous intertidal organisms can be identified in the field without difficulty by reference to these standard authorities. However, some algae cannot be identified in the field, either because identification requires laboratory techniques or because the classification itself is still in doubt. In such cases, the distributional data are provided for the smallest grouping which can be identified in the field (Table I). Specimens were collected from such

groupings and identified later. These specimens have been deposited in the Phycological Herbarium of the University of British Columbia.

Groups of species which presented problems in identification were the Order Ulotrichales (including *Enteromorpha*, *Monostroma*, and *Ulva*); the Family Prasiolaceae (including *Prasiola* and *Rosenvingiella*); and the genera *Spongomorpha*, *Laminaria*, *Costaria*, *Fucus*, and *Gigartina*.

In the Order Ulotrichales it is very difficult, if not impossible, to make a field identification of the less specialized species of *Ulva* and *Monostroma* and the more flattened ones of *Enteromorpha*. Specimens collected of these species were identified later as *Monostroma fuscum* var. *blyttii*, *Ulva lactuca*, *U. taeniata*, *U. lobata*, *Enteromorpha linza*, *E. angusta*, and *E. vexata*. There also were some specimens of *Monostroma*, *Ulva*, and *Enteromorpha* which could not be identified to species. No geographical or vertical pattern could be discerned in the occurrence of these various species.

In the Family Prasiolaceae, it has been shown that *Rosenvingiella* is probably a stage in the life history of *Prasiola* (Friedmann, 1959), and probably a similar relationship exists between the species occurring here (Cole and Akintobi, 1963). In the present study, it was found that the populations were very closely associated in their occurrence in the field, since they characteristically occupy the same zone, and often replace each other at different times of the year.[4]

The intertidal species of *Spongomorpha* in this area is usually *Spongomorpha coalita*, but some of the specimens collected were identified as *S. mertensii* and *S. spinescens*.

Laminaria setchellii is a fairly distinct species, characterized by a heavy, terete stipe which supports the weight of its lamina as it stands in an upright position. It is usually found on exposed coasts, but has been dredged from the subtidal zone in the eastern end of Juan de Fuca Strait. The other species of *Laminaria* were less easy to identify. Reference to Setchell and Gardner (1925, p. 600) indicated that the specimens collected belonged to various forms of *L. cuneifolia* and *L. saccharina*. *Laminaria cuneifolia* usually occurs in areas of moderate surf, while *L. saccharina* is characteristic of more sheltered waters. However, Wilce (1959, p, 166) has shown that *L. cuneifolia* is not the correct name for the species so called by Setchell and Gardner. The author has had the opportunity to observe *L. saccharina* in Europe, where it was originally described. The Atlantic populations of this species also seem to be different from those called by this name in the Pacific, so *L. saccharina* is probably not the correct name for the latter. Moreover, it is difficult to distinguish between "*L. cuneifolia*" and "*L. saccharina*," using Setchell and Gardner's criteria. No further attempt was made to identify these plants here, pending a more authoritative study.

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[4]*Note added in proof*: The identity of *Rosenvingiella constricta* with a stage in the life history of *Prasiola meridionalis* has been confirmed by L. M. Bravo (Studies on the life history of *Prasiola meridionalis*. *Phycologia*, **4**: 177–194, 1965).

Setchell and Gardner (1925, p. 610) and Smith (1944, p. 138) stated that there is one variable species of *Costaria* on this coast, but Doty (1947a, p. 41) listed two species, *C. costata* and *C. mertensii*. *Costaria costata* has a moderately ruffled lamina with an acute base, a costate and distally flattened stipe, and terminal haptera only. *Costaria mertensii* is distinguished by having an amply ruffled blade with a cordate base, a smooth and cylindrical stripe, and accessory haptera formed along part of the stipe as well as the holdfast. Small individuals of either species can be found. *Costaria mertensii* is more often found in sheltered waters. Since a great range of intermediate forms was found, there is some doubt that the two species are genetically distinct. However, without further study, they cannot be said to be synonyms.

Powell (1957) reduced all hermaphroditic species of *Fucus* which have caecostomata to synonymy under *Fucus distichus*. This included two of the species found in Juan de Fuca Strait, *F. evanescens* and *F. gardneri* (better known under the illegitimate name *F. furcatus* C. Agardh). Gardner (1922) listed 34 forms under *F. evanescens* and *F. gardneri* [*furcatus*]. Doty (1947a, p. 45) concluded that most of the forms of *F. evanescens* cannot be usefully distinguished. In the present study, a large number of collections of *Fucus* were made, which were identified with some difficulty as five of Gardner's forms of "*F. furcatus*." These forms seemed to occur completely at random both in respect to season and place, so it seems unlikely that they represent distinct populations. Until the genus is re-examined on the Pacific coast, it is unwise to use any of the relevant subspecific names of *F. distichus*.

Gigartina is a very variable genus in need of further study. The specimens collected from the intertidal zone were identified as *G. agardhii*, *G. cristata*, *G. mamillosa*, and *G. papillata*. These species did not occur in any pattern within their zone, and many intermediate forms were found, so it is not certain that these species are really distinct, or correctly identified.

This study was used to test the theory of critical tidal factors. Doty (1946) developed this theory for the mixed semi-diurnal tides of the Pacific coast of Oregon and California. Mixed semi-diurnal tides are characterized by two high and two low tides during each 25-hr period, all tides usually being of different heights. If the duration of maximum submergence or emergence is plotted against height in the intertidal zone, the resulting curve is not smooth, but shows a series of steps. This means that an organism at a certain height can experience an emergence about twice as long as that which can be experienced by an organism immediately below it. Thus, an organism just above lowest lower high water (LLHW) will be submerged at least once a day, and can experience an emergence of the order of 20 hr. An organism a little lower is always submerged twice a day and can experience a maximum emergence only of the order of 10 hr (Doty, 1957). A similar situation obtains for duration of maximum submergence at such levels as highest higher low water.

Doty (1946) related certain features of the tidal curve, such as LLHW, to these steps in the curve of maximum emergence or submergence against height. He found that breaks, or groups of limits of organisms, tended to occur at

one or other of these related levels. Thus, there are three kinds of level: the feature of the tidal curve, such as lowest lower high water; the step on the plotted curve, such as the increase of maximum emergence from 10 to 20 hr; and the breaks. The theory proposed to relate all three. Doty (1946) reserved the term "critical tidal factor" for a feature of the tidal curve which had been related to a step. Presumably a tidal factor is the feature itself, which may or may not be related to a step. Doty's use of the terms "tidal factor" and "critical tidal factor" is followed in this study. The term "critical level" is avoided, since the limits of individual organisms, rather than the breaks, are considered in this investigation.

Particularly when mixed semi-diurnal tides are being discussed, abbreviations are needed in referring to the various types of high and low tides. The higher and lower high waters of a day are described as HHW and LHW, respectively. Similarly, the higher and lower low waters are given the designations HLW and LLW. In a 14-day tidal period, including both neap and spring tides, each of the above "waters" has a maximum, a minimum, and a mean value, which are designated by prefixing the letters H (for highest), L (for lowest), and M (for mean) to the other three letters. This terminology follows that of Doty (1946) and Scagel (1961).

RESULTS AND DISCUSSION

ENVIRONMENT

The environment in any intertidal zone is exceedingly complex, involving interactions between oceanographic and climatic factors. Any exploratory survey such as the present one must be confined to the most conspicuous and therefore probably most important factors. Those chosen here are salinity and sea temperature, as representative of oceanographic factors; the complex of rainfall, humidity, cloud cover, and hours of bright sunshine as the climatic features; and the tidal rhythms and surf which control the interaction of oceanographic and climatic factors.

Salinity and sea temperature are probably the best known and most conspicuous features of the marine part of the intertidal environment. The summer distributions of surface salinity and sea temperature offshore, which are shown in Fig. 3 and 4, have already been presented by Herlinveaux and Tully (1961). The onshore observations were added in the present study to give a more precise indication of conditions existing on the shore where the organisms live.

It may be seen from Fig. 3 and 4 that there was a good deal of variation in the onshore observations. The winter onshore salinities (Fig. 3A) are much the same as the offshore values. Variation is indicated by occasional lower values, presumably the result of the diluting effect of local run-off. The summer onshore salinities (Fig. 3B) in the western part of the Strait tend to be higher than the offshore values. The higher values are associated with strong westerly winds which are usual in summer (Herlinveaux and Tully, 1961). The lowest sea temperatures observed onshore are similar to the temperatures for the

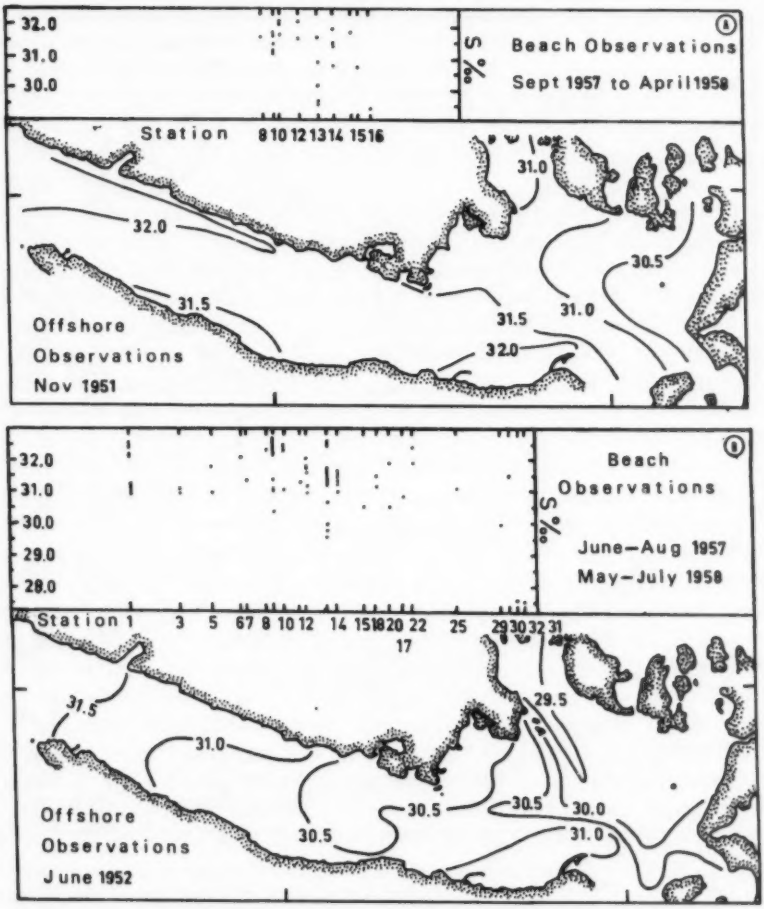

FIG. 3. Surface salinity of Juan de Fuca Strait. Onshore observations made by the author. Offshore observations taken from Pacific Oceanographic Group Data Record (Anon., 1955) (A. Winter; B. Summer).

Strait in general, both in winter and in summer (Fig. 4). Variation in the onshore observations seems to be caused by occasional warming of the water there. In general, the salinity distributions show more differences between different parts of the Strait than do the temperature distributions.

The average yearly rainfall in the area of Juan de Fuca Strait decreases in an easterly direction. It is about 90 inches at Port Renfrew, 30 inches at Race Rocks, and 20 inches in the San Juan Islands. The maximum rainfall is in winter (Anon., 1957).

It is probable that rainfall affects intertidal organisms mostly through its effect on relative humidity and desiccation. Very heavy rainfall was observed

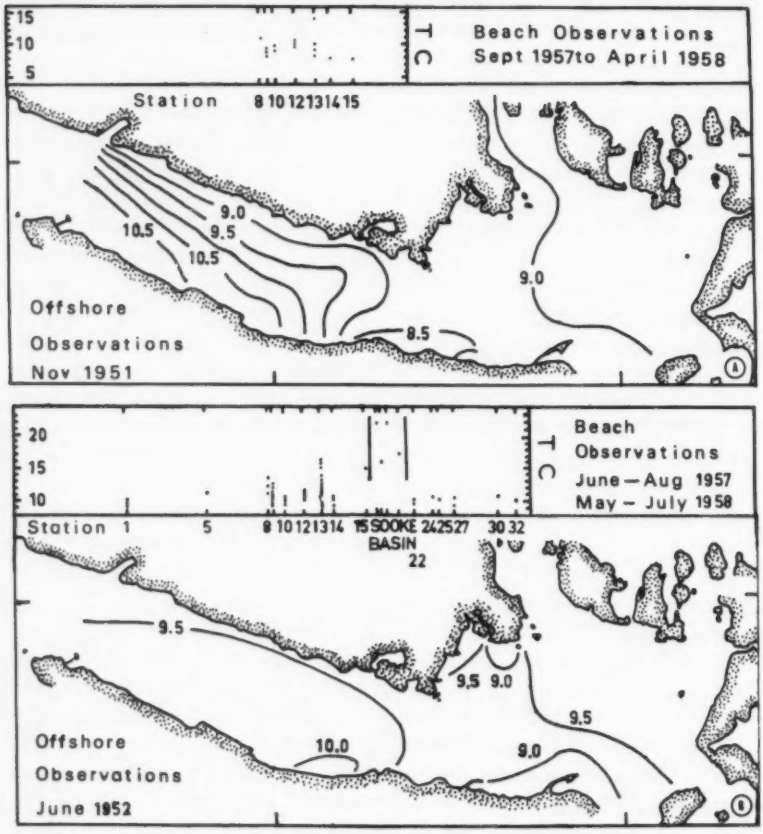

FIG. 4. Surface sea temperature of Juan de Fuca Strait. Onshore observations made by the author. Offshore observations taken from Pacific Oceanographic Group Data Record (Anon., 1955) (A. Winter; B. Summer).

to raise blisters on exposed plants of the Order Laminariales, particularly *Hedophyllum*, but this seems to have no permanent effect.

Rainfall and humidity are roughly related to the amount of cloud cover, which accounts for the differences in incident light at the various localities studied, since the stations are all essentially at the same latitude. The average number of hours of bright sunshine per year is about 1400 at Port Renfrew, 1600 at Sooke, 1800 at Race Rocks, 2000 at Victoria, and 2100 in the San Juan Islands (Anon., 1957).

In areas of heavy surf, near Port Renfrew, the fine spray from breaking waves keeps intertidal organisms moistened with sea water almost every time they are exposed, even on calm, sunny days.

Virtually the full force of the ocean swell reaches the Port Renfrew area from the west. Eastward from Port Renfrew, the intensity of the swell gradually decreases. It is markedly less at Station 10, and usually disappears east of Station 12, in the vicinity of Sooke. This observation applies only to the ocean swell coming from the entrance to the Strait. Very heavy surf from local storms can occur in all parts of the Strait, there being no offshore islands to give shelter.

One 14-day tidal cycle at Port Renfrew and Victoria is shown in Fig. 5. The tidal curve at Sooke is similar to that at Victoria, both in period and amplitude. At Port Renfrew the tides are of the mixed semi-diurnal type. At Victoria they are markedly declinational. The higher low water is not evident for much of the tidal cycle. Since the tidal factors discussed here (Fig. 6D) are derived from a study of the mixed semi-diurnal tide, the tidal factors relating to LHW and HLW at Victoria are probably unreal. The amplitude of large tides is 11.4 ft at Port Renfrew, 10.2 at Sooke, and 9.3 at Victoria.

The mean values in Fig. 6C cannot properly be suggested as critical tidal factors since they are not logically connected with any step in the curves of maximum emergence or submergence. However, it is possible that they may coincide with such steps, and so be of descriptive value. It may be seen in Fig. 6 that various tidal factors are at different relative heights at the various localities. Sooke is intermediate between Port Renfrew and Victoria, except in the case of LLLW. The Sooke tide gauge was situated in Sooke Basin, and the tides recorded there may not be entirely typical of the coast outside at Station 15.

Any critical tidal factors should be apparent from studying Fig. 7. LLHW, HLHW (or LHHW), and HLLW are clearly critical tidal factors at both Port Renfrew and Victoria. However, the critical tidal factors HHLW at Port Renfrew and LLHW at Victoria, although at the same height, are quite different features of the tidal curve, as may be seen in Fig. 6.

The height of the various tidal factors varies throughout the year (Fig. 8), and is made more variable by differing conditions of desiccation and surf.

Distribution of Intertidal Organisms

The vertical and geographical distributions of intertidal organisms were studied with reference to individual species instead of communities. The organisms studied are listed in Table I.

A discussion of the geographical distributions of these organisms requires simultaneous consideration of the distributions themselves, the environmental factors, and the geography of Juan de Fuca Strait. A much simplified outline of the interrelationships between these is shown in Table II.

A number of organisms, such as *Postelsia* and *Lessoniopsis*, are restricted in varying degree to the more exposed coasts in the outer, western part of Juan de Fuca Strait, and so show an "inner boundary" in the area studied. Such geographical distributions are shown in Fig. 9. A smaller number of organisms are restricted, in varying degree, to the sheltered coasts of the inner,

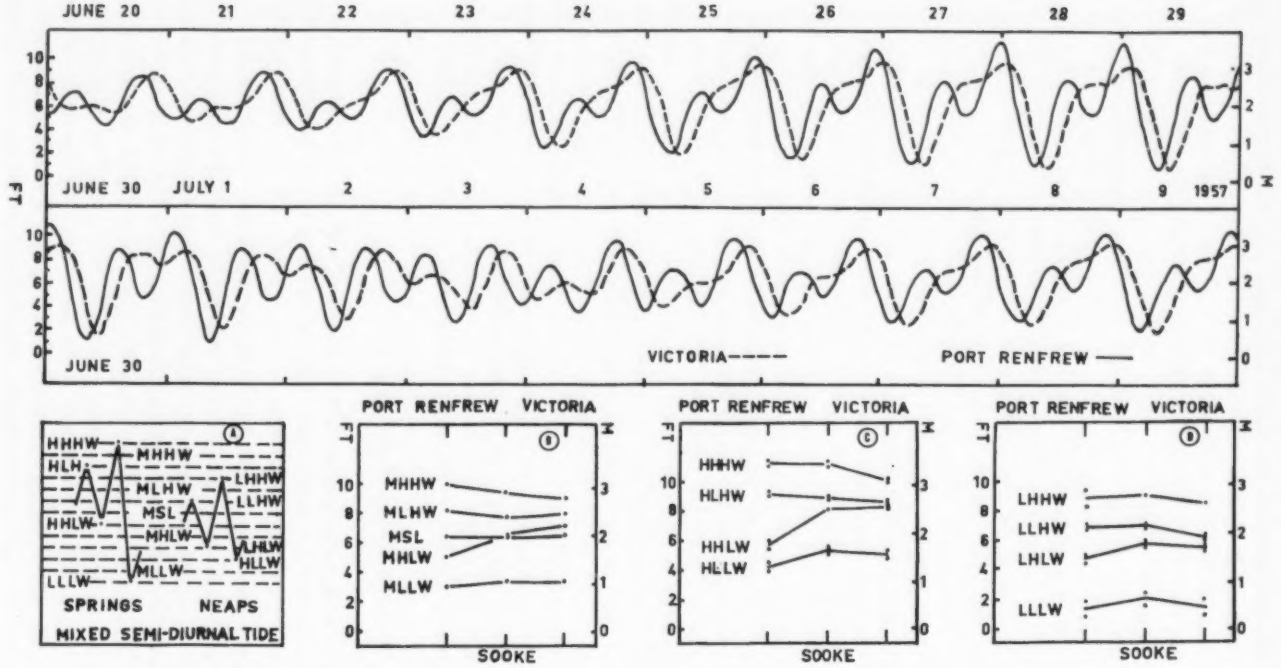

FIG. 5. (*Top*) Curves drawn from hourly coordinates of tide gauges at Victoria and Port Renfrew.

FIG. 6. (*Bottom*) Tidal factors in Juan de Fuca Strait. A. Generalized diagram; B. Mean values; C. Higher values; D. Lower values. (Values in B for Port Renfrew and Sooke taken from 1959 predictions (Anon., 1958); for Victoria, from 1957 predictions (Anon., 1956). Other data for Port Renfrew and Victoria taken from tide gauge coordinates June 18–July 15, 1957; Sooke values extrapolated from those at Victoria.)

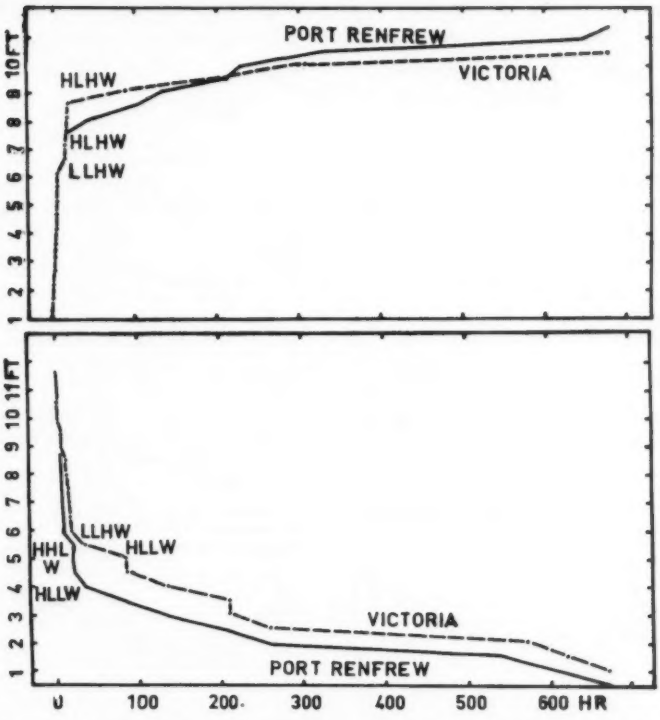

FIG. 7. Hours duration of maximum emergence (*top*) and submergence (*bottom*) as function of height in the intertidal zone. (Taken from tide gauge coordinates June 18–July 15, 1957.)

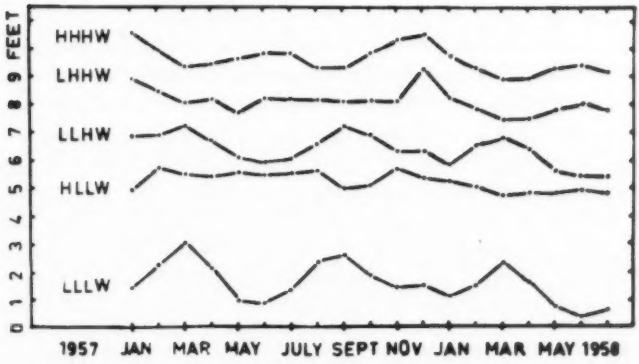

FIG. 8. Variation in height of some tidal factors throughout the year at Victoria. (Taken from the predicted values for each calendar month in 1957 (Anon., 1956).)

TABLE II. Simplified relationships between geography, environment, and distributions.

	Port Renfrew		Sooke		Victoria	
Part of Juan de Fuca Strait	Western outer open				Eastern inner sheltered	
Stations	1–4	5–14	15–20	21–26	27–32	33–34
Salinity onshore	32‰		30‰ sometimes 32‰		30‰ occasionally 27‰	
Hours bright sunshine per year	1400		1600	1800	2000	2100
Surf from ocean swell	Always heavy		Occasional		None	
Tides	Semidiurnal amplitude 11.4 ft		Diurnal amplitude 10.2 ft		Diurnal amplitude 9.3 ft	
Inner limits	*Postelsia* *Pelvetiopsis* *Dictyoneurum*		*Cystoseira* *Macrocystis* *Lessoniopsis* *Alaria nana* *Laminaria setchellii*		*Mytilus californianus* *Alaria marginata* *Egregia* *Mitella* *Phyllospadix* *Hedophyllum*	
Vertical limits	Higher more variable				Not so high less variable	

northeastern part of the Strait, and so show an "outer boundary." Usually these organisms have nearly the same vertical position as a closely related species with an inner boundary in the same area (Fig. 10). The remainder of the organisms studied were found throughout the area. The geographical distributions of these are not illustrated. When their distribution in general throughout British Columbia is taken into consideration (Scagel, 1957), many appear to have an inner boundary not far to the northeast of the area studied, around the San Juan Islands. The other organisms occur also in the Strait of Georgia, and so their geographical distribution may be called general.

The inner boundaries of open coast forms on the southwestern coast of Vancouver Island (Fig. 9 and 10) are mostly separate from one another. In order, from exposed to sheltered, these boundaries are: *Postelsia* (Stn. 1); *Pelvetiopsis* (near Stn. 1); *Dictyoneurum* (Stn. 2); *Cystoseira* (Stn. 15); *Macrocystis* (Stn. 15); *Lessoniopsis* (Stn. 18); *Alaria nana* (Stn. 19); *Laminaria setchellii* (Stn. 20); *Mytilus californianus* (Stn. 27); *Alaria marginata* (Stn. 29); *Egregia* (Stn. 30); *Mitella* (Stn. 31); *Phyllospadix* (Stn. 32); and *Hedophyllum* (Stn. 32). The details of some of these inner boundaries are also different with different organisms. *Lessoniopsis* forms a zone of well-developed plants even at its inner boundary, while *Hedophyllum* becomes more scattered and damaged at the inner parts of its distribution. *Dictyoneurum* has so restricted a dis-

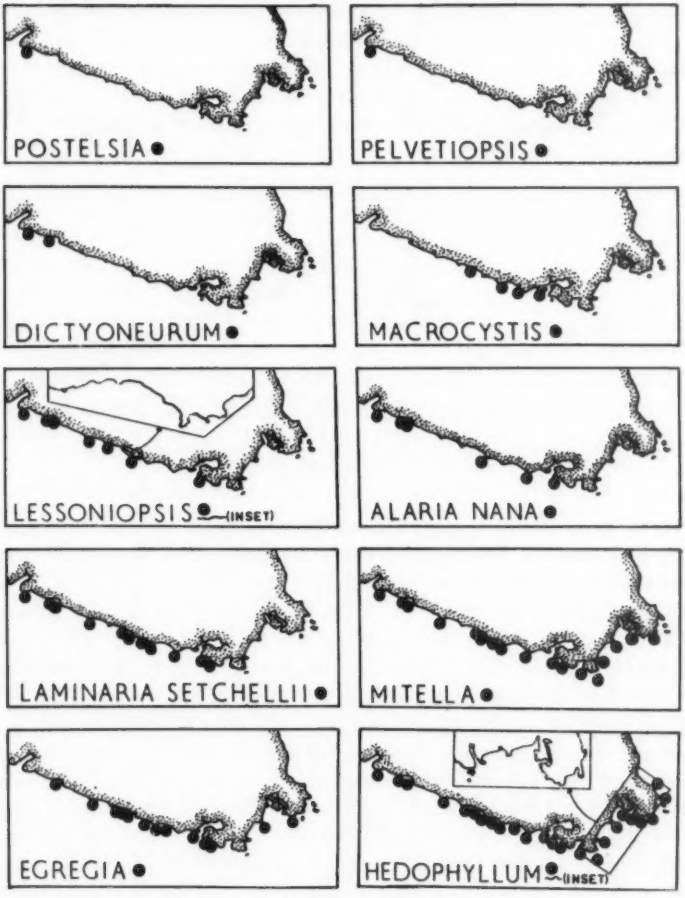

FIG. 9. Geographical distribution of certain open coast organisms in Juan de Fuca Strait.

tribution in British Columbia that an "inner boundary" is perhaps not very meaningful.

Although generally separate, the inner boundaries seem to be grouped in the vicinity of Port Renfrew (Stn. 1–2); Sooke (Stn. 15–20), and Victoria (Stn. 27–32). The transitions between open coast and sheltered coast species (Fig. 10) also occur in these areas. The transitional nature of the Port Renfrew area would be even more apparent if data for inconspicuous open coast forms were included, a number of which probably have inner limits close to Port Renfrew. In the same way, the number of other species which have their inner limits in the San Juan Islands would make the transition zone around Victoria an even more important phytogeographical boundary than this study suggests.

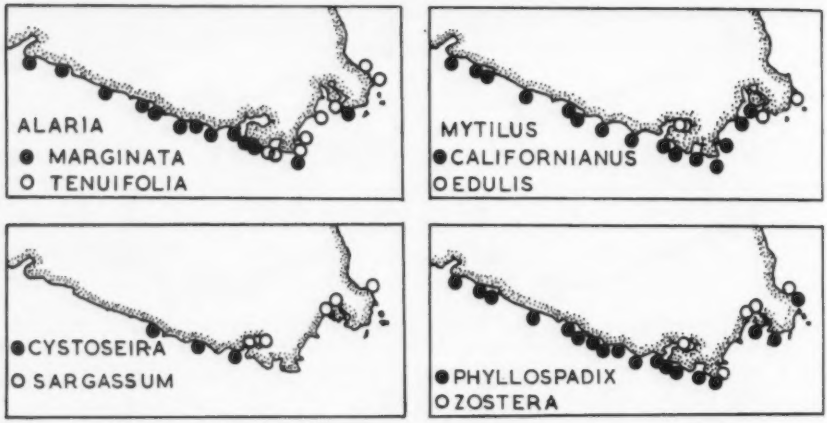

FIG. 10. Geographical distribution of some open coast organisms compared with that of sheltered coast species closely related to them.

There is no *a priori* reason why salinity and sea temperature should be the limiting factors in forming the inner boundaries of benthonic organisms typical of the open coast. However, these water properties form a convenient basis for describing the transition from the open coast to a sheltered one. The salinity distribution shows more differentiation between the sections of coast studied than does the sea temperature, although the high sea temperatures may be important in the scattered areas of very sheltered coast, such as Sooke Basin. Port Renfrew is at the entrance of Juan de Fuca Strait, and is at the eastern end of the strictly open coast, which always has a salinity close to 32‰. The coast from Port Renfrew to Sooke runs in a straight line from northwest to southeast, and under the influence of westerly winds can sometimes experience salinities of more than 32‰. Victoria, on the other hand, is at the southern end of Haro Strait, and is the outermost place where low salinities of less than 30‰ can occur on the beach. This transition at Victoria is shown by Herlinveaux and Tully (1961) as a drop from 15% to 7% in the proportion of fresh water in the upper 10 m of the sea. Unfortunately, experimental evidence is lacking to prove that this connection between salinity and geographical distribution is one of cause and effect, except perhaps in the case of *Mytilus californianus*. Young (1941) found that sex cells and the growth of larvae of *M. californianus* are unfavourably affected by salinities of less than 29.6‰.

In addition to inner boundaries along the coast of Vancouver Island in general, there are boundaries resulting from the absence of outer coast forms in enclosed bays such as Sooke Basin (Stn. 16 and 17), Esquimalt (Stn. 26), and Victoria Harbour (Stn. 28). The eastern shore of the entrance to Sooke Basin is rocky, so that the various inner boundaries can be studied on a small scale there as well as on a larger scale in Juan de Fuca Strait itself (Fig. 12). The positions of the inner limits relative to one another in the two areas can be

roughly compared by arranging both sets in order from most exposed to most sheltered (Table IV). A similar arrangement for the inner limits found in Queen Charlotte Strait by Scagel (1961) is also shown in Table IV. It may be seen that the agreement in the order of limits in the three areas is quite good, suggesting that some general factor in the environment is involved in the formation of inner boundaries.

The horizontal axis of the vertical distributions shown in Fig. 11 was based on the headland–headland distance between stations, on approximately the same scale as that of the maps of geographical distribution. An inspection of the upper and lower limits shows that they differ from one another both in their slope and their variability. Four groups can be distinguished. Firstly, some limits are so variable that no pattern can be observed in them (for instance, the upper limit of *Spongomorpha*). Secondly, some are much more variable in the western part of their distribution (for instance, the upper limit of *Endocladia*). Thirdly, some have a definite and even slope down from west to east (for instance, the upper limit of *Phyllospadix*). Finally, some are virtually constant at all stations (for instance, the upper limit of *Cymathere*).

Each limit, measured to the nearest one-tenth of a foot as y, was plotted against the headland–headland distance between the stations (listed in Table III) as x. The unit selected for this headland–headland distance was arbitrary, the minimum distance between stations being 1 and the total distance from Station 1 to Station 34 being 100. The unit was about 1 mile. A straight line to represent each limit was calculated by the method of least squares. Data from enclosed bays (Stations 16, 17, 26, and 28) were not used in these calculations. The Y-variance of the data from this line of least squares was calculated for the entire coast from Station 1 to 34, and for the two sections Stations 1–15 and 18–34 (Port Renfrew to Sooke, and east of Sooke to east of Victoria).

This approach assumed that a line joining the heights of a limit as measured at each station was linear. The data were not tested for linearity. However, the standard deviation of the data resulting from errors in measurement was calculated independently as about 0.6 ft (p. 1431 above). This would mean that a perfectly linear limit would have a variance of 0.36 from errors of measurement. This should be the minimum variance found, if the figure for the standard deviation is valid and the limits are linear. Actually, the minimum variance should be less, as some of the data are mean values. The smallest variance for the whole coast is shown in the upper limit of *Cymathere*, which is 0.26. The modal variance is between 0.40 and 0.50. Thus, a straight line of least squares must be a good approximation of the less variable limits, which are the ones discussed in detail below.

The difference between the variances along the two stretches of coast, Stations 1–15 (Port Renfrew to Sooke) and Stations 18–34 (east of Sooke), was tested at the 95% level of significance by means of the F ratio. Four limits were found to have a significantly greater variance on the stretch of coast from Port Renfrew to Sooke. These limits are listed in Table V. The total of all the variances along the western stretch of coast is significantly greater than the

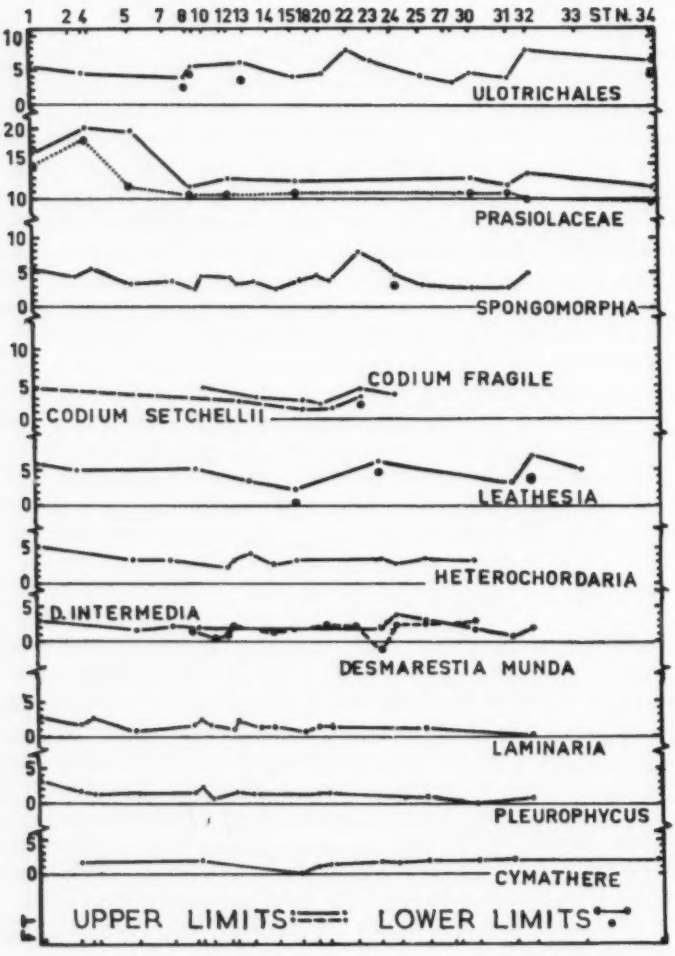

FIG. 11. Vertical distribution of organisms along Juan de Fuca Strait (*continued*).

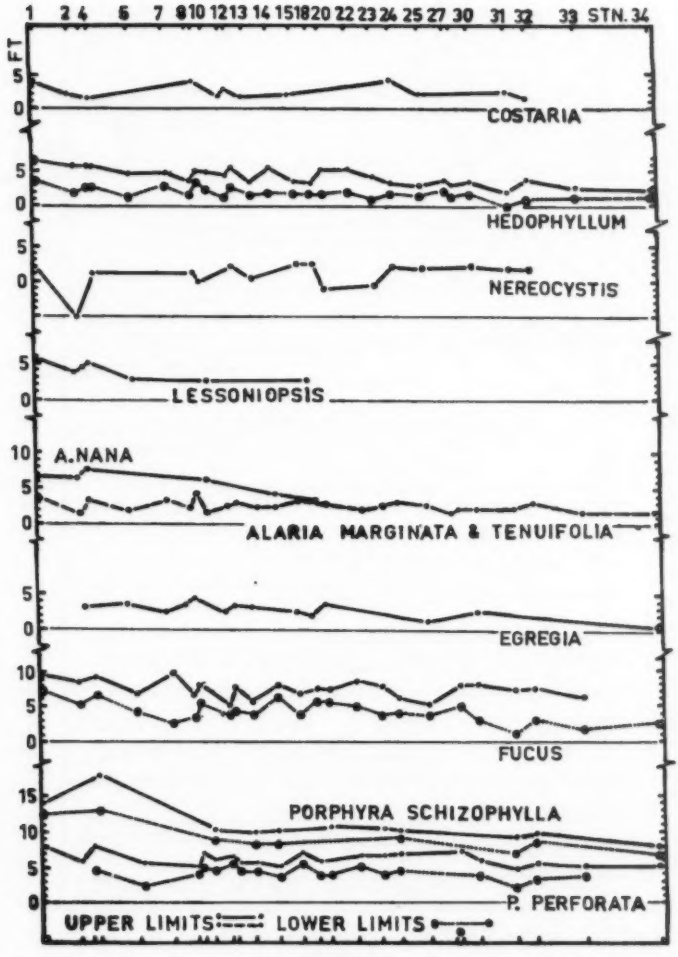

FIG. 11. Vertical distribution of organisms along Juan de Fuca Strait (*continued*).

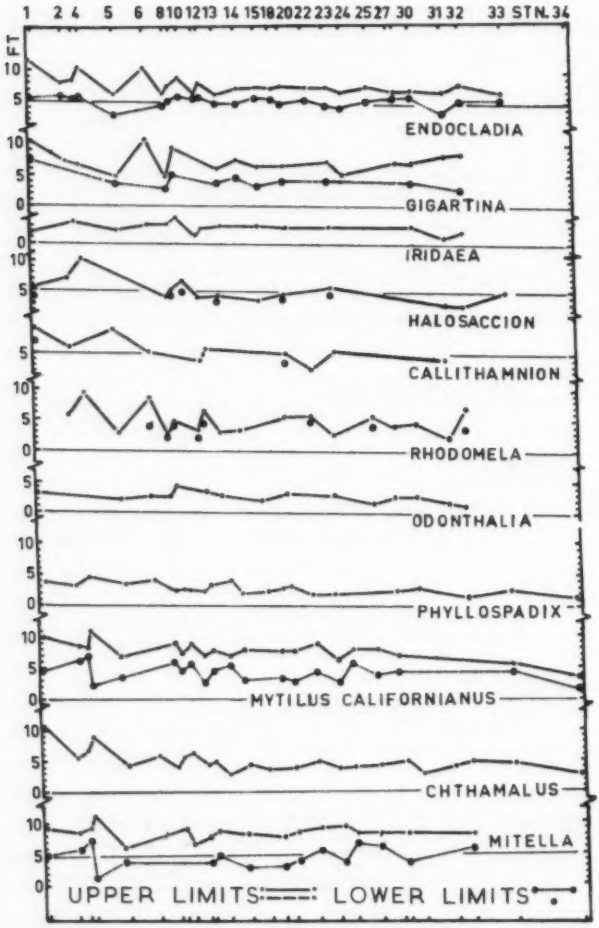

FIG. 11. Vertical distribution of organisms along Juan de Fuca Strait (*concluded*).

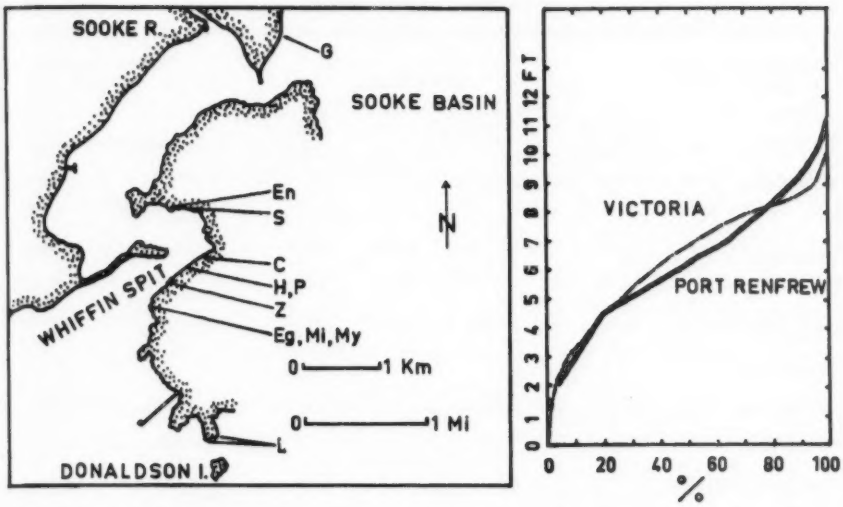

FIG. 12. (*Left*) Inner and outer limits of intertidal organisms along the entrance to Sooke Basin. (G — inner limit of *Gigartina*; En — inner limit of *Endocladia*; S — outer limit of *Sargassum*; C — inner limit of *Cymathere*; H — inner limit of *Hedophyllum*; P — inner limit of *Phyllospadix*; Z — outer limit of *Zostera*; Eg — inner limit of *Egregia*; Mi — inner limit of *Mitella*; My — inner limit of *Mytilus californianus*; L — limits of *Lessoniopsis*.)

FIG. 13. (*Right*) Percentage of time an organism is exposed to air as a function of height in the intertidal zone.

TABLE III. Headland–headland distances of stations.

Station	Distance	Station	Distance	Station	Distance
1	0	11	29	24	58
2	6	12	30	25	63
3	7	13	33	27	67
4	8	14	37	29	68
5	15	15	41	30	71
7	20	18	44	31	77
8	24	20	47	32	80
9	25	22	51	33	88
10	26	23	55	34	100

TABLE IV. Comparison of the order (from exposed coast to sheltered) of inner limits on various British Columbia coasts.

Juan de Fuca Strait–Georgia Strait	Sooke Basin	Queen Charlotte Strait[a]
Postelsia		*Dictyoneurum*
Pelvetiopsis		
		Postelsia
Dictyoneurum		*Pelvetiopsis*
		Lessoniopsis
Cystoseira		*Mitella*
Macrocystis		
Lessoniopsis	*Lessoniopsis*	*Laminaria setchellii*
Alaria nana		*Phyllospadix*
Laminaria setchellii		*Mytilus californianus*
Mytilus californianus	*Mytilus californianus*	*Alaria nana*
Alaria marginata	*Egregia*	*Hedophyllum*
	Mitella	
Egregia		*Egregia*
Mitella		*Cystoseira*
Phyllospadix	*Phyllospadix*	*Macrocystis*
Hedophyllum	*Hedophyllum*	*Alaria marginata*
Cymathere[b]	*Cymathere*	*Cymathere*
Endocladia[b]	*Endocladia*	*Endocladia*
Gigartina[b]	*Gigartina*	*Gigartina*

[a]From Scagel, 1961.
[b]From Scagel, 1957.

total for the eastern stretch. In no case was the variance for the eastern stretch of coast significantly greater than that for the western stretch.

The boundaries of the other three groups were arbitrary. All limits with a variance of more than 1.50, with no significant difference between the variances of the two sections of coast, were placed in the group of variable limits. This group includes 11 limits (Table VI). The variance of 1.50 corresponds to a standard deviation of 1.2 ft, about twice that determined in connection with errors of measurement.

Among the less variable limits, some have a definite slope down from Port Renfrew to Victoria and some have no definite slope. Those limits with

TABLE V. Limits which are more variable on exposed coasts. (The degrees of freedom are listed in parentheses after each variance.)

Limit	Organism	Total variance	df	Variance Stn. 1–15	df	Variance Stn. 18–34	df	Linear constants m	Linear constants b
Upper	*Chthamalus dallii*	1.95	(23)	3.34	(12)	0.47	(10)	−0.044	11.6
Upper	*Endocladia*	1.55	(25)	2.71	(13)	0.32	(11)	−0.032	9.2
Upper	*Prasiola*	5.87	(9)	10.12	(5)	0.74	(3)	−0.079	17.5
Lower	*Prasiola*	3.64	(9)	6.45	(5)	0.18	(3)	−0.059	13.9

TABLE VI. Limits which are very variable along the entire coast.

Limit	Organism	Total variance	df	m	b
Upper	*Nereocystis*	4.30	(15)	−0.006	1.2
Upper	*Rhodomela*	3.77	(12)	−0.027	5.8
Upper	*Porphyra schizophylla*	3.32	(9)	−0.092	15.2
Upper	*Gigartina*	3.29	(14)	0.001	7.4
Upper	*Halosaccion*	2.64	(13)	−0.065	7.8
Upper	*Callithamnion*	2.62	(9)	−0.059	7.5
Upper	*Leathesia*	2.51	(8)	−0.002	4.8
Lower	*Mitella*	2.06	(16)	0.004	4.3
Upper	*Spongomorpha*	1.82	(20)	−0.007	4.6
Upper	Ulotrichales	1.77	(12)	−0.000	4.8
Lower	*Fucus*	1.69	(23)	−0.038	6.5

a slope numerically greater than −0.010 were arbitrarily placed in the group having a definite slope. No positive slopes greater than 0.010 were found. (A slope of −0.010 means that the Y-intercept of the line of least squares is 1 ft lower at Station 34 than at Station 1.) Thirteen limits were found to have a definite slope (Table VII) and eight to have none (Table VIII).

The environmental factor responsible for the greater variability on the open coast (Table V) is probably very closely connected with direct action of surf. The climatic and hydrographic conditions typical of the open coast are relatively constant over a distance of miles, but the action of surf may vary greatly in a

TABLE VII. Slightly variable limits which have a definite slope.

Limit	Organism	Total variance	df	*m*	*b*
Lower	*Gigartina*	1.43	(10)	−0.053	6.2
Upper	*Mytilus californianus*	1.09	(14)	−0.046	9.3
Upper	*Laminaria*	0.48	(14)	−0.049	3.0
Upper	*Hedophyllum*	0.45	(26)	−0.034	5.8
Upper	*Egregia*	0.64	(12)	−0.031	3.9
Upper	*Pleurophycus*	0.36	(13)	−0.025	2.1
Lower	*Hedophyllum*	0.38	(25)	−0.024	2.8
Upper	*Fucus*	1.22	(23)	−0.022	8.1
Upper	*Phyllospadix*	0.33	(21)	−0.020	2.5
Lower	*Mytilus californianus*	1.06	(16)	−0.018	4.4
Upper	*Heterochordaria*	0.93	(11)	−0.017	4.2
Upper	*Porphyra perforata*	1.03	(19)	−0.017	7.0
Upper	*Odonthalia*	0.60	(14)	−0.013	3.1

few yards. This group of limits is a small one and consists of limits in the upper part of the intertidal zone. Thus, surf was found to have a definite effect on some limits. Only certain limits are affected, and the effect is to make them more variable rather than to raise them uniformly. Thus, adding a fixed amount to limits to allow for wave action (Johnson and Skutch, 1928) is probably not a valid procedure.

The very variable limits (Table VI) probably exist for a variety of reasons. *Porphyra schizophylla* is ephemeral, and can spring up and disappear in response to changing conditions at different times of the year. *Gigartina* and *Ulotrichales* are heterogeneous taxonomic groups. The upper limit of *Rhodomela*, which is often associated with tide pools and water seepage, is an example of a limit governed by a factor which is not in a linear relationship to the headland–headland distance between stations.

The limits listed in Tables VII and VIII are the ones most suitable for use in testing the hypothesis of tidal factors. They have been shown to be relatively invariable and unaffected by the direct action of surf. Although it is possible that the other limits are precisely the ones which are more affected by tidal factors, Tables VII and VIII contain more than half of all the limits studied. If the hypothesis has any general use, it must explain these also.

The observed values of each limit for Stations 1, 15, and 30 (Port Renfrew, Sooke, and Victoria) and also the Y-intercepts of the relevant lines of least squares at these three points were used in the test. Any cases where one of

TABLE VIII. Slightly variable limits which have no definite slope.

Limit	Organism	Total variance	df	*m*	*b*
Lower	*Porphyra perforata*	0.52	(15)	−0.010	4.7
Upper	*Costaria*	0.73	(11)	−0.009	2.4
Upper	*Alaria*	0.48	(25)	−0.006	2.8
Upper	*Desmarestia*	0.94	(16)	−0.006	2.1
Lower	*Endocladia*	0.75	(22)	−0.006	5.4
Upper	*Iridaea*	0.67	(14)	−0.006	3.0
Upper	*Mitella*	1.07	(17)	−0.002	8.4
Upper	*Cymathere*	0.26	(9)	−0.002	1.4

these values or intercepts fell within ½ ft of a tidal factor were noted (Fig. 7). If a limit is determined by a tidal factor, it should coincide with that factor at all three of the localities studied.

Out of the 20 limits used, four coincided with a tidal factor. These were the upper limits of *Desmarestia* and *Cymathere* (LLLW), of *Porphyra perforata* (LLHW), and of *Mitella* (HLHW). It is possible that these are simple coincidences, but it is easy to see why LLLW may be an important critical tidal factor. Some algae, of which *Desmarestia* (Mųenscher, 1915) is a good example, cannot survive even a few minutes of drying. Even on the open coast there are occasional calm, sunny days. Over the period of a month or two, such a day would probably coincide with a low tide. Thus, an alga which cannot survive any degree of drying would probably be limited by LLLW in spite of the dampening effect of surf and a moist climate. A number of limits parallel LLLW but are a little distance above it: the upper limits of *Costaria* (b = 2.4), *Alaria marginata* and *A. tenuifolia* (B = 2.8), and *Iridaea* (b = 3.0). These may be plants which are slightly more resistant to drying, or which are smaller and can be more sheltered by other plants. Since some time is required for a plant to dry, limits dependent on LLLW should be a little above it rather than at exactly the same level. These limits which are a little above LLLW are well approximated by MLLW. This latter is often quoted as a critical tidal factor, even though strictly it is not one, not being connected with any sudden increase in maximum emergence.

The hypothesis of critical tidal facts, except for LLLW, does not seem to be generally useful either as an explanation or as a detailed description of intertidal limits. It is probable that in special cases a tidal factor may have an important effect. However, the hypothesis has so far been used as a general explanation or description, and should be judged as such.

Most of the limits listed in Table VIII are probably related to LLLW as a critical tidal factor. The others retain such a constant height in such different

environments that they are probably associated with a mean rather an extreme value of a factor in the environment. One such mean value is the percentage of time a level is exposed (Fig. 13). A possible mechanism by which the percentage of time exposed could limit an organism involves nutrients. It would not make much difference to the nutrition of an animal or plant if in any particular day it is exposed for a maximum of 6 or 12 hr. However, a change from 50% exposure to 55% exposure might make a great difference to the feeding of the one or the absorption of nutrients by the other. The concentration of nutrients in the sea water around British Columbia coasts is relatively high and is probably not often limiting to phytoplankton. However, the surface-to-mass ratio of a benthonic alga is much smaller than that of a phytoplankter. In addition, an intertidal alga is exposed for some time, when it cannot absorb nutrients. So, nutrients may very well be limiting to intertidal benthonic algae.

The slightly variable limits which have a distinct slope (Table VII) are the most difficult of all to explain. In the case of *Laminaria*, an upper limit appears to start in the low intertidal zone at Station 1 and cross low water mark into the subtidal zone in the San Juan Islands. This example indicates that some factor may be involved which is not peculiar to the intertidal zone. The only environmental factor which appears to have a regular gradient from Port Renfrew to Victoria is incident light, measured as hours of bright sunshine. (Decreased clarity of sea water at Victoria, relative to Port Renfrew, might, however, reduce this gradient.) Chapman and Trevarthen (1959) have shown how the restrictions placed on photosynthesis by desiccation and lack of light may limit an intertidal alga in its upper and lower levels, respectively. More light in the vicinity of Victoria could cause a lowering of lower limits, both in the intertidal and the subtidal zones. Desiccation as a hindrance to photosynthesis and other life functions might operate on upper limits. This effect of desiccation would work over a relatively long period, so that mean values of surf and humidity would be involved. This should result in a relatively even slope. This effect of desiccation should not be confused with desiccation as a directly lethal factor. This latter would operate as a function of extreme values of surf and humidity, and would result in a much more variable limit.

CONCLUSION

The relative positions of inner limits of organisms in Juan de Fuca Strait, compared to the corresponding relative positions in Sooke Basin, and Queen Charlotte Strait (Scagel, 1961), and the vertical limits of each organism at different stations along the Juan de Fuca Strait show a large degree of consistency. It therefore should be useful to search for general causes for these distributional features.

The geographical distribution of intertidal organisms in Juan de Fuca Strait is most easily described in terms of salinity, although proof of a causal effect is lacking in most cases. Several factors appear to be involved in the determination of the vertical distribution of organisms; in consequence, vertical limits fall into

several categories on the basis of their variability and height in the various parts of the Strait. With none of these categories does the theory of critical tidal factors have a general descriptive value.

ACKNOWLEDGMENTS

The author wishes to thank Dr R. F. Scagel of the Institute of Oceanography University of British Columbia for his direction and helpful criticism; the Fisheries Research Board of Canada for the grant of a Bursary during the period 1957–58; and the Canadian Hydrographic Service for providing tide gauge data.

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Effect of Thermal Acclimation and Sublethal Heat Shock Upon Ionic Regulation in the Goldfish, *Carassius auratus* L.[1,2]

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ABSTRACT

Goldfish acclimated to 20 and 30 C exhibited no significant differences in plasma sodium level, tissue chloride, potassium and water content, and chloride space. Plasma chloride varied inversely and plasma potassium directly with temperature. Tissue sodium levels tended to be slightly lower at the higher acclimation temperature. The shock response following abrupt transfer from 20 to 30 C was characterized by a complex sequence of changes in water–electrolyte balance. Following a lag period plasma chloride rose sharply, peaking some 48 hr after transfer, and subsequently declining. Plasma sodium varied in substantially similar fashion. Changes in plasma sodium/chloride ratio suggested the possible occurrence of a transient condition of alkalosis following thermal shock. Plasma potassium levels increased rapidly, and appeared to stabilize within 24 hr. By contrast, little variation in tissue levels of sodium, potassium, and chloride was observed. Tissue water content, on the other hand, tended to increase steadily for several days after transfer. Changes in chloride space suggested that an increase in extracellular phase volume, in part at the expense of the cellular fluids, accompanied thermal shock. It is concluded that while thermal shock induces marked initial deviations in iono- and osmoregulatory ability the goldfish can, during the acclimatory process, carry out compensatory changes in regulatory activities which permit restoration of virtually the original ionic status. Possible mechanisms underlying the shock and acclimatory responses are discussed, and the bearing of studies of this general type upon the estimation of thermal acclimation rates is considered.

INTRODUCTION

Despite the emphasis placed in recent years upon the investigation of thermal relationships in fishes (Fry, 1957, 1958, 1964) relatively little is known of the influence of environmental temperature upon water–electrolyte metabolism and regulation in these animals (Wikgren, 1953; Gordon, 1964; Parry, 1964). This is somewhat surprising in view of the well-documented thermosensitivity of most of the physiological activities of teleosts.

A series of investigations emphasizing the effects of low temperatures has, however, demonstrated that exposure to acute or lethal cold is usually associated with some degree of osmoregulatory failure. Thus, both Doudoroff (1945) and Brett (1952) have provided evidence suggestive of an osmoregulatory involvement in the death of the killifish, *Fundulus parvipinnis*, and sockeye salmon,

[1]Received for publication August 5, 1964.

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J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

Oncorhynchus nerka, at temperatures close to their lower incipient lethal levels. Impairment of plasma chloride regulation has been observed in freshwater-adapted lamprey, *Petromyzon fluviatilis*, and carp, *Cyprinus carpio*, exposed to temperatures ranging from 1 to 3 C (Wikgren, 1953). A generalized loss of regulatory capability is seen in cod, *Gadus morhua*, *G. callarias*, taken from sea water near 2 C (Woodhead and Woodhead, 1958, 1959). Meyer *et al.* (1956) and Houston (1962) have recorded changes in plasma and tissue ion levels, and in the tissue water content and distribution of goldfish, *Carassius auratus*, held at temperatures between 2 and 4 C.

While less attention has been directed toward the effects of acute temperature increase a recent investigation (Heinicke and Houston, 1965) has demonstrated that marked decreases in plasma chloride and significant increases in tissue hydration and extracellular phase volume accompany heat death in goldfish.

The impact of temperature variations within the normal tolerance zone has also received some attention, primarily in studies upon animals believed to be acclimated to the test temperatures employed. Hoar and Cottle (1952), for example, observed a direct relationship between tissue water content and temperature in goldfish acclimated to temperatures ranging from 5 to 35 C. Raffy (1952, 1954) examined the effects of temperature upon osmotic regulation in several freshwater and marine teleosts, while Phillips (1962) investigated blood phosphorus levels in brook trout, *Salvelinus fontinalis*, held at temperatures between 8 and 16 C. More extensive investigations have been carried out upon brown trout, *Salmo trutta*, and rainbow trout, *S. gairdneri*, acclimated to 10 and 20 C, and 6 and 16 C, respectively (Gordon, 1959; Hickman *et al.* 1964). Notwithstanding differences in detail these studies suggest that the species tested are capable of relatively high levels of osmotic, and more particularly ionic, regulation over the intermediate ranges of their zones of thermal tolerance.

Thus, studies carried out to date leave little doubt as to the thermosensitivity of teleostean water–electrolyte metabolism, but on the other hand also indicate that the animals can, when acclimated, maintain a remarkably constant ionic status over at least restricted ranges of environmental temperatures. At present, however, little is known of the changes in ion metabolism and regulation which accompany the thermal acclimation process. A single study upon rainbow trout acclimated to 16 C and exposed to a 10 C decrease in temperature has, nevertheless, clearly demonstrated the complexity of the osmo- and ionoregulatory correlates of cold acclimation (Hickman *et al.* 1964).

The absence of information upon this point constitutes a gap of some importance in the understanding of thermal relationships in teleosts. The influence of body fluid ionic composition upon physiological activity has been well reviewed upon several occasions (e.g. Manery, 1954; Comar and Bronner, 1960 *et seq.*), and it is apparent that alterations in the ionic composition of the extracellular and cellular fluids are frequently reflected by changes in cellular and organ system function. It was, therefore, with the aim of providing

a more detailed picture of the regulatory sequelae of the thermal shock response and thermoacclimatory process that the present study was undertaken.

In order to maximize the consequences of such changes temperature variations were applied as abruptly as possible. Such a procedure necessitated employment of a species of considerable thermal tolerance, and the highly eurythermal goldfish was consequently selected as a test animal. The basic protocol of the investigation involved acclimation of the animals to a base temperature of 20 C, followed by their transfer to 30 C. The work of Fry *et al.* (1942) upon this species had originally suggested that shifts of greater magnitude might be employed. However, several preliminary trials indicated that abrupt transfers from 20 C to temperatures in excess of 35 C proved rapidly lethal to many animals of the stocks employed. Consequently a 20–30 C shift was used routinely during the study. Subsequent to transfer analyses of plasma and tissue levels of sodium, potassium, and chloride were carried out in order to follow changes in ionic regulation. As in previous studies (Houston, 1962; Houston and Threadgold, 1963) the stability of tissue water distribution was taken as a criterion of osmotic regulation. The basis for this lies in the high level of water permeability characteristic of most cellular membranes. Because of this, transient or continuing changes in the relative solute concentrations of cellular and extracellular fluid phases, or in membrane permeability, must lead to osmotic exchanges tending to restore concentration equilibrium. Thus, variations in tissue fluid distribution should provide as reliable an indication of changes in internal osmotic relations as the more commonly employed freezing point depression of the plasma.

MATERIALS AND METHODS

Origin and Maintenance of Stocks

Fish used in the study were obtained from the Goldfish Supply Company, Stouffville, Ontario, in lots of 200–300 animals. They were maintained at the University in continuously aerated, fiberglass-lined wooden tanks of approximately 80 liters capacity. Water temperatures were held at either 20.0 ± 0.1 or 30.0 ± 0.1 C through the use of thermistor-activated electronic relays. Five hundred watt copper-sheathed resistance heaters were wrapped with Teflon tape to minimize ionic contamination of the tank water. In view of the known effects of photoperiod upon the thermal resistance of this species (Hoar and Robertson, 1959) the tanks were completely hooded and illumination provided on a 12-hr light–dark schedule. The animals were fed daily *ad libitum* on commercial dry cereal supplemented with liver paste, and remained in active and apparently healthy condition throughout the investigation.

Experimental Protocol

All animals were held for a minimum of 3 weeks at 20 C prior to use, an interval which upon the basis of Brett's work (Brett, 1946) upon this species seemed sufficient to insure complete acclimation.

Acclimation to 30 C was established by transfer of fish to this temperature from 20 C. Again, an interval of not less than 3 weeks was allowed before sampling for completion of the thermoacclimatory process.

Thermal shock was induced by direct transfer of fish from 20 C acclimation tanks to tanks held at 30 C. The animals were shifted in water with a minimum of handling since it has been well established that marked disturbance of teleostean water–electrolyte metabolism is readily entrained by handling procedures (Meyer, 1948; Forster and Berglund, 1956). Groups of fish were subsequently taken for sampling at 12-hr intervals for 96 hr, and thereafter at 24-hr periods for up to a total of 240 hr. The values reported represent data obtained in from two to four such trials.

Sampling

Individual fish were anesthetized before sampling in aqueous tricaine methanesulphonate (M.S. 222), the concentration of which was adjusted as required to produce narcotization within 5 min. Blood samples were obtained by bleeding caudally-transected fish into polyethylene dishes lightly dusted with dry disodium or dipotassium ethylenediaminetetraacetate (EDTA) to prevent coagulation. Heparin, used by Anthony (1961) and oxalate used by Field *et al.* (1943) were found to be unsatisfactory. All blood samples were immediately centrifuged at 10,000 rpm for 4 min, and the plasma pipetted off and stored frozen until required for analysis. Haemolyzed specimens were discarded. Muscle tissue samples were obtained from both epaxial muscle bands, and rapidly dissected free of obvious scales, skin, connective tissue, and bone fragments. Water content was determined by drying samples to constant weight at 105 C. The dried samples were then wrapped in Parafilm and stored frozen until used for analysis.

Analytical Procedures

All plasma determinations were performed in duplicate or triplicate using Lab-Trol (Fisher Scientific Company) as a reference standard.

Plasma chloride estimation was carried out on 10-μliter samples by means of a micromodification of the mercurimetric titration procedure of Schales and Schales (1941) using a buffered citrate dilutant.

Tissue chloride determinations were based upon the modified "open Carius" procedure of J. F. Manery (1955, personal communication). Dried tissue samples were soaked overnight in 0.02 N silver nitrate, and subsequently digested for at least 8 hr in concentrated nitric acid, to which hydrogen peroxide and potassium persulphate were periodically added. Capping the digestion tubes with glass spheres tended to reduce loss of chloride in the form of volatile chloride-containing digestion products (Shenk, 1954). Residual silver ion was estimated by thiocyanate titration using ferric alum indicator. The addition of 1 ml of nitrobenzene to each sample immediately prior to titration markedly improved the stability of the endpoint.

Plasma samples were diluted 1:200 (v/v) for potassium, and 1:100 (v/v) for sodium determinations with aqueous lithium chloride, and measurements made by means of a lithium internal-standard flame spectrophotometer (Advanced Instruments Company) against bracketing standards. Dried tissue samples were digested in concentrated nitric acid, diluted with lithium chloride as appropriate and analyzed in the same fashion.

Phase Volume Estimation

Values for "chloride space" were used as estimates of extracellular phase volume, and were calculated by means of the relationship described by Manery (1954):

$$(1) \ldots\ldots\ldots H_2O^{ecs}_{Cl^-} = (t^{Cl^-}/p^{Cl^-})\ (pH_2O)\ (rCl^-)$$

where: $H_2O^{ecs}_{Cl^-}$ = chloride space, g/kg muscle tissue
t^{Cl^-} = tissue chloride concentration, mmole/kg
p^{Cl^-} = plasma chloride concentration, mmole/liter
pH_2O = plasma water content (taken as 950 g/liter)
rCl^- = 0.977 (Manery, 1954):

This method of estimating extracellular phase volume, like the "sodium space," is open to the criticism that the presence of some chloride in the cellular fluids of muscle tissue (Conway, 1957; Cotlove and Hogben, 1962) results in overestimation of phase volume. The "chloride-potassium space" derived by Conway (1957), and used in some studies on fish tissues (Houston, 1959; Hickman *et al.*, 1964) yields values more in accord with those obtained by other methods. It is, however, based upon the questionable assumption that potassium and chloride are distributed between cellular and extracellular fluids in accordance with the Donnan relationship. The application of this method to fish muscle has been criticized by Gordon (1959) among others. On the other hand, the small size of the animals employed and the sensitivity of teleostean water–electrolyte metabolism to physical disturbance seemed to preclude estimation of extracellular phase volume through the use of substances requiring prior administration or serial blood sampling, and to rule out employment of the most generally accepted measure of extracellular phase volume, the "inulin space." "Chloride space" values have, therefore, been accepted as a reasonable compromise, providing at least an indication of extracellular phase volume, and of the changes in tissue fluid distribution induced by thermal shock.

Cellular phase volume was estimated as the difference between chloride space and tissue water content:

$$(2) \quad \ldots\ldots\ H_2O^{ics}_{Cl^-} = {}_tH_2O - H_2O^{ecs}_{Cl^-}$$

where: $H_2O^{ics}_{Cl^-}$ = cellular phase volume, g/kg

${}_tH_2O$ = tissue water content, g/kg.

Statistical Procedures

In instances where the number of values obtained in each sample group were regarded as sufficient, group means and standard deviations were determined by the methods outlined by Goldstein (1964). In other cases means and ranges only have been reported. Assuming the data to obey a Gaussian distribution all values falling outside the range defined by the mean ± two standard deviations were discarded, and the group mean, variance, standard deviation, and standard error calculated for each data set.

Several methods were employed in data comparison. Initially the variance estimates of the sample groups, taken in pairs, were compared by the variance ratio or F-test (Goldstein, 1964). Means of the sample groups, taken in pairs, were then compared by the Fisher extension of the Student *t*-test, or the Cochran and Cox procedure as appropriate (Johnson and Jackson, 1959). Significance was attached to sample groups whose means varied at the 0.05 level.

Inasmuch as it was not always possible to carry out determinations of both plasma and tissue chloride content upon individual fishes, values for chloride space were based upon group mean values for these parameters. The mean and 95% confidence interval for each group was then estimated by the method of Goldstein (1964). Groups were regarded as significantly different at the 0.05 level when their confidence limits did not overlap.

RESULTS

Fish Acclimated to 20 and 30 C

Values for plasma and tissue concentrations of sodium, potassium, and chloride, tissue water content, chloride space, and cellular phase volume are recorded in Table I for fish acclimated to 20 and 30 C for periods of not less than 21 days.

It would appear that no significant variation attributable to the acclimation process took place in plasma sodium, tissue chloride, and potassium, and tissue water content and distribution. However, acclimation to the higher temperature was associated with small, but significant, decreases in plasma chloride and tissue sodium levels, and some increase in the plasma concentration of potassium.

Effects of Thermal Shock Upon Ionic Regulation and Water Balance

PLASMA COMPOSITION

Values obtained for plasma chloride, sodium, and potassium levels following transfer of fish from 20 to 30 C are summarized in Table II and presented graphically in Fig. 1.

TABLE I. Plasma and tissue composition and tissue water distribution in goldfish acclimated to 20.0±0.1 C and 30.0±0.1 C for 3 weeks or more.

Acclimation temperature (*C*)	Plasma constituents		
	Plasma chloride (*mmole/liter*)	Plasma sodium (*mmole/liter*)	Plasma potassium (*mmole/liter*)
20	82.0±0.8, (74.5–89.5), 25[a]	175±9, (138–234), 18	6.1±0.6, (3.0– 8.7), 10
30	78.5±1.5, (67.2–90.4), 15	155±8, (122–189), 11	8.3±0.3, (7.1–10.6), 10
Significance	0.05[b]	N.S.	0.05
	Tissue constituents		
	Tissue chloride (*mmole/kg*)	Tissue sodium (*mmole/kg*)	Tissue potassium (*mmole/kg*)	Tissue water (*g/kg*)
20	19.3±1.4, (9.4–34.8), 28	7.7±0.5, (2.9–12.2), 21	104±4, (83–150), 27	807±2, (793–829), 28
30	17.4±0.9, (12.3–23.1), 16	4.7±0.8, (1.5–12.3), 14	115±6, (67–147), 16	808±4, (794–845), 15
Significance	N.S.	0.05	N.S.	N.S.
	Tissue water distribution		
	Extracellular phase volume		Cellular phase volume
20	218, (183–255), (27.0)[c]		589 (73.0)[d]
30	206, (182–230), (25.5)		602 (74.5)

[a]Mean ± standard error, (range), sample size.
[b]Level of significance (Students *t*-test).
[c]Mean, (95% confidence interval), (percentage of total tissue water).
[d]Mean, (percentage of total tissue water).

TABLE II. Plasma chloride, sodium, and potassium levels in goldfish acclimated to 20 C and abruptly transferred to 30 C.

Exposure to 30 C (*hr*)	Plasma chloride (*mmole/liter*)	Plasma sodium (*mmole/liter*)	Plasma potassium (*mmole/liter*)
12	81.2±1.2, (78.5– 85.2), 6[a]	–	9.5 , (8.8–10.6), 3
24	80.1±1.5, (75.6– 84.7), 7	177 , (134–213), 4	9.2 , (4.1–12.3), 4
36	84.5±2.7, (79.6– 95.5), 7	202 , (160–247), 3	13.2 , (11.5–16.3), 3
48	104.2±1.2, (101.9–108.8), 6	221±11, (196–254), 5	8.9 , (8.0– 9.9), 3
60	87.8±3.3, (77.3– 97.2), 6	213 , (153–272), 2	–
72	83.1±3.2, (67.3– 96.2), 8	255 , (209–280), 3	9.9 , (8.0–11.0), 3
84	80.1±0.7, (78.0– 82.0), 7	252±23, (195–302), 6	11.0±0.9, (9.3–13.5), 5
96	81.6±1.5, (76.0– 92.3), 15	242 , (185–312), 3	–
120	76.5±0.2, (75.0– 77.5), 10	205 , (162–242), 4	–
144	78.0±0.8, (75.2– 81.8), 10	–	–
168	79.2±1.4, (76.0– 86.1), 9	–	–
192	78.9±0.5, (76.7– 81.1), 8	–	–
216	76.5±1.1, (71.7– 81.1), 9	–	–
240	78.6±0.9, (74.7– 81.9), 8	–	–

[a]Mean ± standard error, (range), sample size.

Chloride values (Fig. 1A) remained relatively stable for a period of approximately 24–36 hr after exposure to the increased temperature. An abrupt increase to a mean of 104.2±1.2 mmoles/liter at 48 hr then took place. Following this peak chloride concentration dropped sharply, reaching values comparable to those seen in the 20 C acclimated fish after 60–72 hr. Chloride levels from 120 to 240 hr ranged from 76.4±0.2 to 79.2±1.4 mmoles/liter in the different groups sampled. The means for groups taken during this interval were comparable to those seen in fish acclimated to 30 C (78.5±1.5 mmoles/liter), but lower than the value characteristic of 20 C animals (82.0±0.8 mmoles/liter).

Plasma sodium variations are summarized in Fig. 1B. The small volume of blood obtainable from many of the fishes precluded replicate estimates of plasma ion concentrations. Consequently, the response pattern obtained for sodium, and also for potassium, is considerably less complete than that for chloride. Nevertheless, even the limited series of data available indicate substantially the same sequence of changes in plasma sodium as was seen in plasma chloride following thermal shock. Thus, a lag period of some hours ensued prior to any change. Thereafter the plasma sodium concentration rose steadily, reaching maximum levels between 72 and 96 hr after transfer. The single

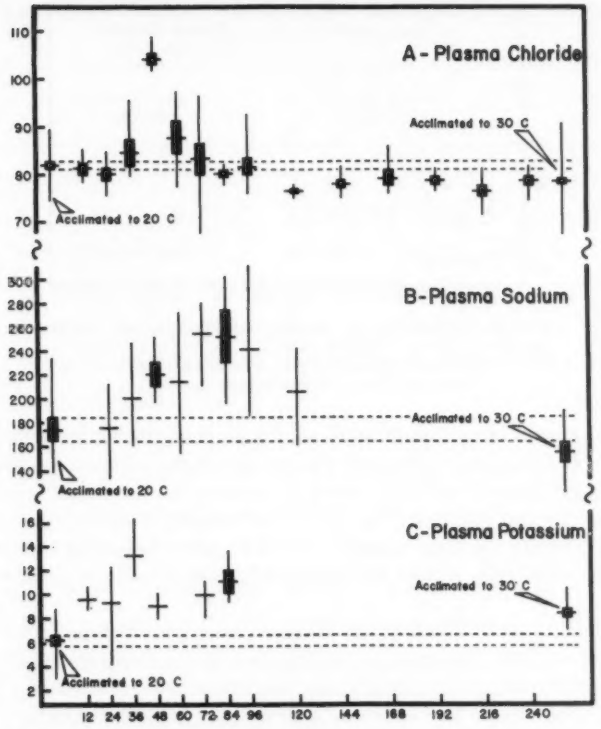
A - Plasma Chloride
Acclimated to 30 C
Acclimated to 20 C
B-Plasma Sodium
Acclimated to 30 C
Acclimated to 20 C
C-Plasma Potassium
Acclimated to 30 C
Acclimated to 20 C
12 24 36 48 60 72 84 96 120 144 168 192 216 240

FIG. 1. Variation in plasma chloride (A), sodium (B), and potassium (C) following abrupt transfer from 20 C to 30 C. *Cross bar* — sample mean; *solid vertical bar* — one standard error of the mean; *vertical line* — sample range. *Ordinate* — mmole/liter; *abscissa* — hours exposure to 30 C.

group of four values obtained at the 120-hr sampling period suggested that a subsequent decrease in concentration was initiated at that time. Comparison of the 20 and 30 C acclimation groups indicated that this secondary trend led to the eventual restoration of plasma sodium values essentially comparable to those characteristic of the original situation.

While both sodium and chloride levels rose transiently following thermal shock their rates and magnitudes of change differed. As a consequence, variations in plasma sodium–chloride ratio took place (Fig. 2). The value for 20 C animals was comparable to the values noted between 24 and 48 hr. At the 60-, 72-, and 84-hr sampling periods, however, the sodium-chloride ratio rose sharply to a maximum of 3.14. Subsequent decreases at 96 and 120 hr then took place, while the ratio in 30 C acclimated animals was close to that seen in the 20 C control group. Assuming the condition of body fluid electroneutrality to hold following thermal shock these changes suggest the likelihood of compensatory

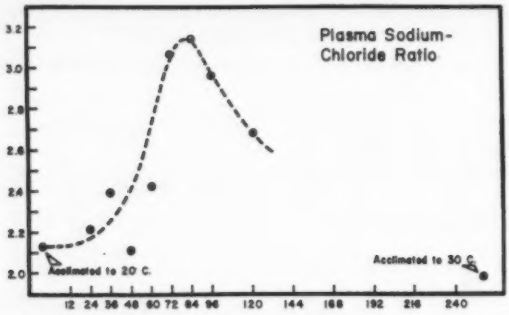

FIG. 2. Variation in plasma sodium:chloride ratio following abrupt transfer from 20 to 30 C. *Ordinate* — plasma sodium (mmole/liter) — plasma chloride (mmole/liter); *abscissa* — hours exposure to 30 C.

increases in plasma bicarbonate level, and with this, the possible establishment of a transient condition of alkalosis during the thermal shock response.

Plasma potassium content varied in somewhat the same fashion as had plasma chloride and sodium (Fig. 1C). The means of all the groups sampled between 12 and 96 hr after transfer to 30 C were well above that observed in 20 C acclimated fish, as was the value characteristic of the group acclimated to 30 C.

The effect of heat shock upon plasma electrolyte composition was, then, characterized in each instance by an increase in concentration. Plasma chloride, which remained fairly steady for the initial 36 hr, showed the greatest increase, but by 120 hr had fallen to a new steady level somewhat lower than the original concentration. Sodium also increased after a lag interval of about the same duration, and peaked between 84 and 120 hr after thermal shock. The final plasma sodium level in the 30 C acclimated fishes was, however, not significantly different from that observed in the animals acclimated to the lower temperature. Finally, plasma potassium concentration increased almost immediately, and remained above the level characteristic of 20 C acclimated fishes.

TISSUE COMPOSITION

Results obtained from tissue determinations are recorded in Table III and Fig. 3.

With the exception of samples taken at the 36- and 84-hr periods, tissue chloride levels (Fig. 3A) did not show significant variation during the 240-hr test period. The mean tissue chloride concentration of fish held at 30 C for at least 21 days, 17.4 ± 0.9 mmoles/kg, did not differ significantly from that seen in the 20 C control group.

Tissue sodium, like tissue chloride did not vary significantly over the test period (Fig. 3B). However, the tissue sodium level characteristic of animals acclimated to 30 C for 3 weeks, 4.7 ± 0.8 mmoles/kg, was significantly

TABLE III. Tissue chloride, sodium, and potassium concentrations in goldfish acclimated to 20 C and abruptly transferred to 30 C.

Exposure to 30 C (*hr*)	Tissue chloride (*mmole/kg*)	Tissue sodium (*mmole/kg*)	Tissue potassium (*mmole/kg*)
12	16.6±2.4, (12.1–26.5), 6[a]	9.5±1.9, (6.7–14.0), 6	127±16, (95–188), 6
24	14.5±1.6, (7.5–20.0), 7	8.8±0.9, (7.1–11.4), 5	118±12, (85–158), 7
36	14.5±1.4, (9.8–19.9), 7	8.8±1.0, (5.9–12.5), 6	123± 6, (99–141), 7
48	20.3±2.2, (14.3–26.0), 6	11.8 , (7.2–18.0), 4	112± 9, (92–139), 6
60	22.1±3.0, (13.4–30.7), 6	7.2 , (6.0– 8.4), 4	118± 9, (96–146), 6
72	17.8±1.1, (13.0–21.1), 8	10.1±1.8, (4.7–18.6), 8	105±10, (79–146), 9
84	11.6±1.0, (9.5–13.1), 7	–	121± 8, (107–144), 7
96	22.1±4.3, (13.2–49.7), 12	8.2±1.4, (5.0–14.1), 6	112± 5, (92–128), 7
120	21.2±2.1, (10.0–31.7), 11	12.5±3.3, (6.8–26.4), 5	112± 7, (85–130), 6
144	23.2±3.8, (7.8–48.3), 11	8.9 , (8.1– 9.8), 2	133± 8, (104–155), 6
168	31.3±5.8, (13.1–58.2), 9	–	112 , (92–133), 2
192	29.3±6.1, (11.2–59.3), 9	16.3 , (5.6–35.4), 3	73 , (39– 96), 3
216	23.9±3.6, (14.0–41.1), 7	10.6 , (5.8–15.4), 2	–
240	32.0±6.4, (11.0–60.2), 9	4.5 , (1.7– 8.6), 3	98 , (86–115), 3

[a]Mean ± standard error, (range), sample size.

lower (but only barely so at the 0.05 level) than the value observed in goldfish acclimated to 20 C, 7.7±0.5 mmoles/kg.

A generally comparable situation was seen with respect to tissue potassium content (Fig. 3C), although a barely significant increase in concentration was recorded in the 36-hr sample. The average tissue potassium levels of fish acclimated to 20 C (104±4 mmoles/kg) and 30 C (115±6 mmoles/kg) did not differ significantly.

Tissue ionic composition, then, appeared to be remarkably stable following thermal shock. Only in the instance of sodium was there a significant concentration variation associated with acclimation to the higher temperature.

TISSUE WATER CONTENT AND DISTRIBUTION

While tissue electrolyte levels appeared to be relatively conservative in the face of thermal shock this was not true of tissue water content. Almost all groups of animals sampled between 24 and 240 hr after transfer to 30 C were characterized by tissue water levels considerably higher than those observed in fish acclimated to 20 C (Table IV, Fig. 4A). A single exception was

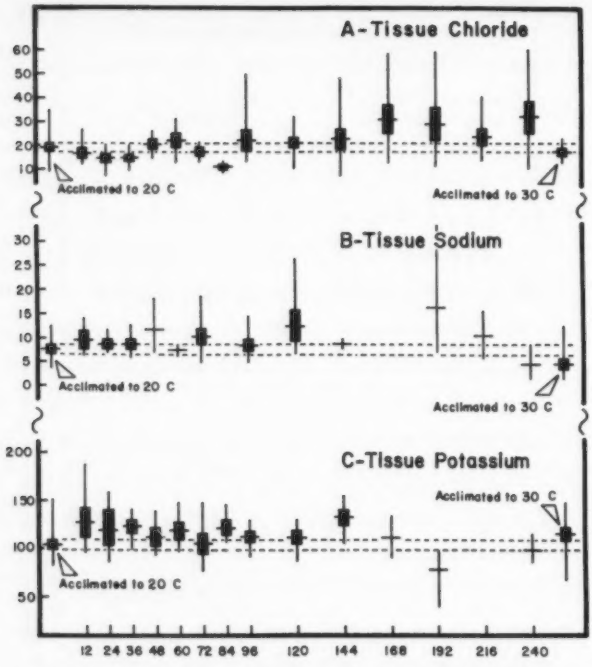

FIG. 3. Variation in tissue chloride (A), sodium (B), and potassium (C) following abrupt transfer from 20 to 30 C. *Cross bar* — sample mean; *solid vertical bar* — one standard error of the mean; *vertical line* — sample range. *Ordinate* — mmole/kilogram; *abscissa* — hours exposure to 30 C.

seen in the group of fish taken at the 84-hr period. A more or less steady increase in water content took place with a peak being reached some 168 hr after transfer. Thereafter tissue water level declined, and the level observed in the 30 C group, 808 ± 4 g/kg, was almost identical to that recorded for fish acclimated to 20 C (807 ± 2 g/kg).

Changes in chloride space are summarized in Table IV and Fig. 4C. The wide dispersion of values for goldfish transferred from 20 to 30 C precludes any strong inference regarding changes in tissue water distribution. The general trend of values suggests, however, that an increase in extracellular phase volume accompanied thermal shock. Corresponding values for tissue water content minus chloride space (Fig. 4B) suggest, furthermore, that extracellular phase volume increases might be in some part associated with a shift of cellular fluids into the former compartment. However, the major contribution to an increased extracellular fluid volume would seem to be water taken up by osmosis and localized in that tissue area.

TABLE IV. Tissue water, chloride space, and tissue water–chloride space in goldfish acclimated to 20 C and abruptly transferred to 30 C.

Exposure to 30 C (*hr*)	Tissue water (g/*kg*)	$H_2O^{ecs}_{Cl^-}$ (g/*kg*)	$H_2O^{tcs}_{Cl^-}$ (g/*kg*)
12	825± 9, (808–860), 6[a]	190, [126–254], (23.0)[b]	635, (77.0)[c]
24	817± 5, (802–836), 7	168, [121–216], (20.6)	649, (79.4)
36	821± 5, (802–838), 7	160, [121–199], (19.5)	661, (80.5)
48	836± 7, (820–856), 6	182, [134–229], (21.8)	654, (78.2)
60	833± 6, (814–845), 6	236, [129–341], (28.3)	598, (71.7)
72	827± 4, (814–845), 8	195, [161–229], (23.6)	632, (76.4)
84	813± 5, (801–828), 6	135, [105–164], (16.6)	679, (83.4)
96	848±10, (811–928), 14	276, [183–369], (32.5)	572, (67.5)
120	835± 4, (808–851), 11	258, [201–314], (30.9)	577, (69.1)
144	845± 8, (820–899), 11	276, [178–375], (32.7)	569, (67.3)
168	885±16, (834–946), 9	368, [217–518], (41.6)	517, (58.4)
192	863±16, (817–924), 9	345, [169–521], (40.0)	519, (60.0)
216	875±13, (834–925), 9	291, [192–389], (33.3)	584, (66.7)

[a]Mean ± standard error, (range), sample size.
[b]Mean, [95% confidence interval], (percentage of total tissue water).
[c]Mean, (percentage of total tissue water).

DISCUSSION

The values obtained in this study were, in general, comparable to those reported in earlier studies on this and a related species of carp, *Cyprinus carpio* (Field *et al.*, 1943; Nishihara, 1953; Meyer *et al.*, 1956; Houston, 1962). However, in the case of plasma chloride concentration there was some discrepancy between the levels recorded in the present investigation and those cited. The means for animals acclimated at 20 and 30 C, 82.0±0.8 and 78.5±1.5 mmoles/liter, respectively, were some 30–40 mmoles/liter lower than those reported for goldfish (Houston, 1962), carp (Field *et al.*, 1943), brown trout (Gordon, 1959), and Atlantic salmon (Houston and Threadgold, 1963), although comparable to the whole blood values given by Nishihara (1953) for this species. The basis for this is not apparent, since substantially the same maintenance, handling, and analytical procedures were employed in an earlier investigation (Houston, 1962), and all determinations were made against the same type of reference standard.

Tissue water levels were nearly identical to those reported by Hoar and Cottle (1952) and Meyer *et al.* (1956) for the goldfish. However, because of the relatively low plasma chloride values, estimates of extracellular phase

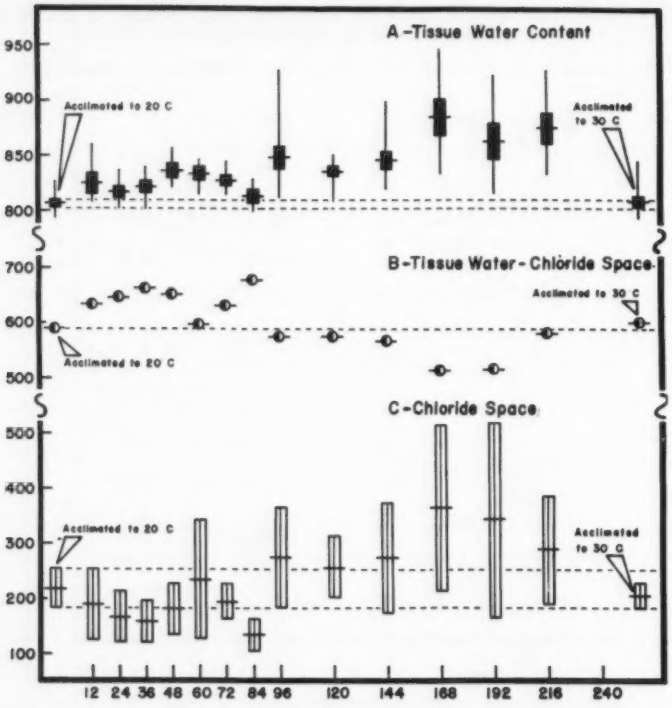

FIG. 4. Variation in tissue water content (A), tissue water content minus chloride space (B) and chloride space (C) following abrupt transfer from 20 to 30 C. *Cross bar* — sample mean; *solid vertical bar* (A) — one standard error of the mean; *open vertical bar* (C) — 95% confidence interval of the mean; *vertical line* (A) — sample range. *Ordinate* — grams/kilogram; *abscissa* — hours exposure to 30 C.

volume tended to be somewhat larger, and cellular phase volumes correspondingly lower than those previously reported for the goldfish (Houston, 1962), and the related carp, *Cyprinus carpio* (Thorson, 1961). They fall, nevertheless, within the ranges observed in fishes (Thorson, 1961), and other vertebrates (Dittmer, 1961).

Ionic Composition Following Thermal Acclimation

The data for the 20 and 30 C groups suggest that the goldfish has a well-developed capacity to regulate its ionic composition at differing environmental temperatures. Although some variation was apparent in the plasma and tissue concentrations of each electrolyte studied, the changes were either insignificant, or of slight magnitude. The most obvious variations were seen with respect to plasma chloride, which decreased by 3.5 mmoles/liter (−4.3%), and plasma potassium which increased from 6.1 ± 0.6 to 8.3 ± 0.3 mmoles/liter (+36.1%).

A barely significant decrease in tissue sodium was also observed. Plasma sodium, tissue potassium, and tissue chloride, on the other hand, showed no significant change.

Studies upon the brown trout (Gordon, 1959) and rainbow trout (Hickman *et al.*, 1964), while differing in some details agree in indicating that the capacities of these species to regulate ionic composition are not substantially altered by thermal acclimation. However, the three species show some differences in ability to regulate specific electrolyte levels. Thus, a survey of the values presented by Gordon (1959) for groups of brown trout held at 10 and 20 C indicates no consistent variation in plasma chloride with temperature. Rainbow trout (Hickman *et al.*, 1964) resemble goldfish in that an inverse relationship is seen between plasma chloride concentration and acclimation temperature. Rainbow trout, on the other hand, did not exhibit the increases in plasma potassium concentration observed in goldfish and brown trout.

A comparable situation may be seen with respect to tissue levels of these ions. Gordon (1959) attached no significance to variations between the tissue sodium contents of 10 and 20 C acclimated brown trout, while Hickman *et al.* (1964) observed that the tissue level of this ion was lower in rainbow trout held at 6 C than in those acclimated to 16 C. In the goldfish tissue sodium was slightly but significantly lower at 30 than at 20 C. Tissue potassium levels tended to be higher in brown trout maintained at 20 than in those held at 10 C, whereas in rainbow trout tissue potassium tended to vary inversely with temperature. The goldfish, however, showed no significant variation in tissue potassium content at 20 and 30 C. All three species were similar in the absence of significant changes in tissue chloride concentration.

As regards other electrolytes Hickman *et al.* (1964) found little difference between the plasma levels of calcium, magnesium, and phosphate in rainbow trout held at 6 and 16 C. Similarly, Gordon (1959) did not regard differences in the total phosphorus values of 10 and 20 C acclimated brown trout as significant. Phillips (1962) on the other hand, reported a well-defined relationship between blood phosphorus and temperatures between 8 and 16 C in the brook trout.

The significance of these differences in capacity to regulate individual ion levels remains, at present, uncertain. It would seem reasonable to conclude, however, that these teleosts, at least, are able to maintain remarkably constant ionic composition over quite broad temperature ranges. The functional importance of this capability, particularly as far as neuromuscular and similar functions are concerned would seem to be immediately obvious.

Water Content and Distribution Following Thermal Acclimation

A similarly well-developed ability to control tissue water content and distribution was also observed in these three species. As previously noted, the water content and "chloride space" values observed in goldfish held at 30 C were almost identical to those recorded in 20 C fish. Gordon (1959) also

TABLE V. Representative values for plasma and tissue electrolyte levels in *Carassius auratus* and *Cyprinus carpio*.

Species	Plasma			Tissue					References
	Cl^-	Na^+	K^+	Cl^-	Na^+	K^+	H_2O	Extracellular volume	Cellular phase volume	
Carassius auratus	81.5[a]	–	–	5.3	–	–	–	–	–	Nishihara (1953)
C. auratus	–	–	–	–	249.7±36.3[b]	276.5±31.1[b]	790.3±14.3	–	–	Meyer *et al.* (1956)
C. auratus	123.1	–	–	15.8	–	–	803.3	122[c]	681	Houston (1962)
Cyprinus carpio	113[d]	130	6.2	–	–	–	–	–	–	Field *et al.* (1943)
C. carpio	–	–	–	–	–	–	714 12	155 33[e]	559	Thorson (1961)

[a]Whole blood.
[b]Milligrams per kilogram dry tissue.
[c]Based on chloride space.
[d]Given as whole blood NaCl.
[e]Based on sucrose space.

found close agreement between the tissue water levels of brown trout maintained at 10 and 20 C, while plasma-to-tissue chloride ratios, which approximate "chloride space" estimates, were similar in the two groups. The values reported for tissue water in 6 and 16 C acclimated rainbow trout (Hickman *et al.*, 1964), appeared to be comparable. Interpretation of the data was, however, complicated by the occurrence of a significant difference between the tissue water levels reported for two samples of 16 C trout. Values for both "chloride space" and "chloride-potassium space," however, agreed well in the two acclimation groups.

In an earlier study Hoar and Gottle (1952) reported a direct relationship between tissue water content and temperature in goldfish acclimated to temperatures ranging from 5 to 35 C. These authors also cite unpublished studies by V. S. Black on the same species, in which the water content of 13 animals held at 11–26 C was some 20 g/kg higher than that of fish maintained at 2–11 C. While the protocols of these investigations differed from that of the present study the discrepancy between the findings of these authors and those cited above, and the marked and prolonged increases noted in goldfish transferred from 20–30 C raise the possibility that the fish used by Hoar and Cottle and by Black, may not have achieved the steady state condition at the time of sampling.

Water–Electrolyte Balance Following Thermal Shock

Whatever the situation in thermally-acclimated animals, it is apparent that thermal shock induces sharp deviations from the regulated state. No comparable studies upon this aspect of the effect of nonlethal temperature increase are known to the authors. It was, however, of some interest to note that Gordon (1959) attributed the unusually high plasma chloride levels observed in one group of brown trout held at 20 C to their incomplete acclimation to this temperature following transfer from hatchery troughs with water temperatures " . . . near 10 C . . . ." The comprehensive investigation of the effects of nonlethal cold shock upon rainbow trout by Hickman *et al.* (1964), however, has demonstrated an equally dramatic pattern of response to temperature change in this species. Moreover, despite procedural differences some striking similarities in response may be observed in goldfish and rainbow trout. The cold-shocked trout resembles the heat-shocked goldfish in the development of transient peaks in plasma sodium and chloride concentration, and in the occurrence of slower changes in tissue water level. Thus, while profound differences in other features exist, there may be some basis for the suggestion that certain aspects of the shock response are generalized in character, and are independent of the direction of temperature change.

Mechanisms of the Thermal Shock Response

Although the nature of the data obtained in the several investigations so far carried out does not permit detailed analysis of the mechanisms involved,

several hypotheses have been advanced in attempts to account for the osmo- and ionoregulatory sequelae of lethal and tolerated changes in environmental temperature. Wikgren (1953), for example, believed that differential changes in water and ionic permeability coupled with variations in kidney function would account for the loss in ionic regulation observed in cold-shocked lamprey and carp. Meyer *et al.* (1956) emphasized the possible role of changes in water permeability, and decreases in the activity of ion transport processes at low temperatures. Houston (1962) raised the possibility that the decline in plasma chloride seen in goldfish exposed to lethal cold might be a consequence of differential, temperature-induced variations in the activity of cellular and extracellular water molecules, and of changes in surface tissue water permeability. Finally, Hickman *et al.* (1964) suggest that many of the transient changes in ion levels observed in rainbow trout during cold acclimation may result from a massive escape of cellular electrolytes into the extracellular compartment.

Undoubtedly temperature changes affect membrane permeability, kidney function, and ion transport systems. The possible complexities which may be encountered have been indicated by the work of Huf and Doss (1959) on the relationship between temperature and sodium-potassium transport by frog skin. Here transport rates were found to reach a maximum near 20 C, and to be significantly diminished at both higher and lower temperatures. Thermally-associated changes in the rate of metabolic production of organic and inorganic solutes and water may also play a role in the establishment of osmotic gradients. Similarly, changes in the activities of cellular and extracellular water molecules and ions due to differential cooling or heating of these two compartments may supplement metabolic effects. In addition, the differential thermosensitivities of nervous and hormonal regulatory systems as demonstrated by Fortune (1958), Mahon *et al.* (1962), Roots and Prosser (1962), and Konishi and Hickman (1964) have as yet been scarcely considered in relation to the regulation of water–electrolyte metabolism.

The interpretation of thermally-related changes in water-electrolyte balance thus becomes exceedingly difficult in the absence of detailed information regarding the effects of temperature upon the many components of the teleostean osmo- and ionoregulatory mechanisms. For example, increases in plasma sodium and chloride levels as seen in goldfish, and to some extent in rainbow trout, might be regarded as the result of temperature-induced changes in surface permeability and branchial salt transport. However, it is at least equally conceivable that renal function changes leading to decreased glomerular filtration rates, or to increased tubular electrolyte reabsorption, or to both could achieve the same result. Several alternate hypotheses including those of Houston (1962) and Hickman *et al.* (1964) are also possible. Inasmuch as similar reasoning may be applied to most of the effects observed in thermal shock responses the need for more detailed dynamic studies upon the several processes involved in osmoregulatory metabolism and its control requires little emphasis.

Estimation of Thermal Acclimation Rates

Finally, some comment may be made with respect to the more general features of the phenomenon of thermal acclimation in fishes. Many of the consequences of this process have been defined in terms of overt effects such as changes in incipient lethal temperatures, resistance times at extra-incipient lethal temperatures, oxygen consumption, locomotor performance, and thermal preference reactions (Fry, 1957, 1958, 1964). Several investigations have suggested something of the biochemical events associated with thermal acclimation (Ekberg, 1958; Freed, 1965; Kanungo and Prosser, 1959; Hochachka and Hayes, 1962; Fenwick and Houston, unpublished data). Acclimatory changes in nervous system function and endocrine activity have also been the subject of some study (Fortune, 1958; Mahon *et al.*, 1962; Roots and Prosser, 1962; Konishi and Hickman, 1964). Little attention has, however, been directed toward the assessment of the rate at which thermal acclimation is achieved (Brett, 1956).

It would seem likely that a basic feature of the acclimatory process is the re-establishment of dynamic equilibria among processes whose rates are differentially influenced by temperature variations. Thus, a measure of acclimation rate may be based upon the time required for the organism to reach a new stationary state following a change in state-influencing environmental conditions. Sprague (1963) operating upon what would appear to be this principle has defined acclimation rates in several species of freshwater crustaceans in terms of rates of change in heat tolerance. Allanson and Noble (1964) have also used this approach in an investigation of thermal acclimation in the cichlid, *Tilapia mossambica*. Determinations of this type are of fundamental ecological importance. Other approaches are, however, both possible and useful. Since all expressions of thermal acclimation rates must find their bases in cellular events, an alternate criterion may lie in the determination of the time required for the restabilization of the internal environment, since it is in context with this that cellular activities take place. Seemingly such restabilization must be achieved prior to, or in accompaniment with, the cellular and systemic changes which allow increases or decreases in thermal resistance, activity, and similar overt expressions of acclimation.

Of the data obtained in the present study those related to plasma ion concentrations and tissue water content and distribution would seem to be the most useful. Reference to Fig. 1A suggests that stabilization of extracellular chloride levels required not less than 120 hr. Extrapolation of the limited series of values for plasma sodium and potassium (Fig. 1B, C) and plasma sodium–chloride ratios (Fig. 2) indicates that equilibrium in these instances was not reached until some 144–192 hr after transfer to 30 C. Tissue water content and distribution, on the other hand, had not achieved the steady state situation at the end of 10 days, although it would appear that stabilization was reached by 3 weeks. Thus, even the limited data of the present investigation and those arising from the study on cold acclimation in rainbow trout (Hickman *et al.*, 1964) indicate that the process of thermal acclimation may

involve longer periods of time than have been previously suggested (Brett, 1946).

ACKNOWLEDGMENTS

Much of the work reported herein was carried out with the financial support of a contract between the Fisheries Research Board of Canada and the University of Manitoba, while one of us (E.A.H.) received additional support in the form of a Fisheries Research Board of Canada post-graduate studentship award. This support, and that of the National Research Council of Canada is gratefully acknowledged, as is the interest and encouragement of Dr W. A. Kennedy, Director, Fisheries Research Board of Canada Biological Station, London, Ontario.

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Supplementary Checks on the Scales of Pink Salmon (*Oncorhynchus gorbuscha*) and Chum Salmon (*O. keta*)[1]

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ABSTRACT

Among 159 central British Columbia pink salmon that had been marked by removal of two fins as fry and had been recovered in commercial fisheries after one winter in the sea, the scales of about one-third showed a supplementary or "false" check near the centre of the scale, in addition to the single clear-cut annulus. This evidence from fish of known age confirms the prevailing opinion that such extra checks do not represent annuli, hence that the fish bearing them are in their second year of life rather than their third. Unmarked pink salmon from the same area, and some from southern British Columbia, had a generally similar incidence of supplementary checks. In both marked and unmarked fish the supplementary checks varied in distinctness from faint to quite clear. In a sample of scales of 14 double-fin marked chum salmon which were known to be in their 4th year, all fish had the expected 3 annuli, and 12 fish had a supplementary check inside the first annulus.

INTRODUCTION

Pink salmon are characterized by a very short life cycle and rapid growth, when compared to the other species of Pacific salmon. In North America it has long been generally accepted that nearly all pink salmon mature in their second year of life (Gilbert, 1914; Anas, 1959). A typical pink salmon scale has widely-spaced circuli near the centre (focus), which are interpreted as representing the first summer's growth in the ocean. These are followed by a band of closely-spaced circuli, considered to represent the growth in the ocean during the first winter, so that the outer edge of this check is the annulus.[2] Outside of the annulus is a second group of widely-spaced circuli, representing the growth in the second summer in the ocean prior to the spawning migration (Fig. 1).

On some pink salmon scales an additional check has been observed nearer the focus of the scale (Fig. 2–4). It also occurs on some chum salmon scales. This inner check has been interpreted by most investigators as a supplementary check rather than a winter check. Miyaguchi (1959) uses the term "fry zone" to describe this check and the area inside it. He states that the frequency of this fry zone is higher in some runs than in others, and suggests that it is formed

[1]Received for publication April 6, 1965.

[2]Scales of salmonid fishes usually are marked by alternating bands of widely-spaced and closely-spaced circuli (margins of the sclerites). The term *check* is used here to refer to any such zone of closely-spaced circuli. *Winter check* will refer to any check that is interpreted as representing a winter season of slow growth. The outer margin of a winter check will be called the *annulus*.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

as a result of physical change in the environment. In the USSR also, most authors have interpreted this inner check as something other than a true winter check, for example Eniutina (1962).

Recently, however, two scientists have taken a different view. Vedensky (1954) and Lapin (1963) both consider that the inner check is neither a fry zone nor anything supplementary, but is actually a true winter check. Vedensky believed he could recognize on most scales not only this inner check but still another check as well, and hence considered that pinks were usually age 4 at maturity. Lapin is more conservative; his interpretations of the scales of certain Asian stocks of pink salmon suggest that a variable but sometimes fairly large proportion of each brood matures at 3 years of age, the balance maturing at 2 years. While it is certainly possible that Asian pink salmon stocks may differ from North American stocks in this respect, the photographs published by Vedensky, Eniutina, and Lapin show scale patterns that are very similar to those of British Columbia pinks.

Thus it seems worthwhile to reexamine the hypothesis that the "inner" checks on scales of British Columbia pink salmon (and chum salmon) are not true annuli, particularly since an opportunity for an unequivocal test has arisen recently. In 1961, Dr R. R. Parker of the Fisheries Research Board of Canada Biological Station, Nanaimo, conducted a large-scale marking program on pink and chum salmon fry of the 1960 brood year, in Statistical Area 8 of the central coast of British Columbia. Many of these marked pinks returned to Area 8 in 1962 as maturing individuals (Fig. 5). Examination of scales taken from some of these fish makes it possible to check scale structure against the known age of these fish.

PROCEDURE AND METHODS

Marked Fish

Most of the young salmon handled in the spring of 1961 were marked by removal of two fins. The "BV" mark (removal of both ventral fins by close clipping) was given to 421,500 young pink salmon at Hook Nose Creek, Port John, King Island, in the Bella Coola region of the central British Columbia coast (Statistical Area 8). Another group of young pinks was captured in salt water in nearby Fisher Channel, a branch of Fitz Hugh Sound, and 36,900 of these were marked by removal of the adipose and right ventral fins (AdRV) (Parker, 1964).

In 1962, special observers stationed at canneries examined 1,160,645 of the pink salmon caught in that general area. They obtained 5997 typical BV marks and 184 typical AdRV marks (Parker, 1964). "Typical" marks are those in which the fin scars have the normal appearance characteristic of closely clipped fins: that is, individuals with slightly damaged fins, or with fins and pelvic girdle entirely absent, were not included among the fish designated as having been marked.

However, even typical marks do not necessarily all represent authentic fin-clipped fish. For the present purpose we must be assured that these adult

FIG. 1. Typical scale from a marked adult pink salmon showing the absence of a supplementary check and the winter check (B).

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FIG. 2. Scale from a marked adult pink salmon, showing a "faint" supplementary check (A) and the winter check (B).

FIG. 3. Scale from a marked adult pink salmon, showing a "fair" supplementary check (A) and the winter check (B).

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FIG. 4. Scale from a marked adult pink salmon, showing a "good" supplementary check (A) and the winter check (B).

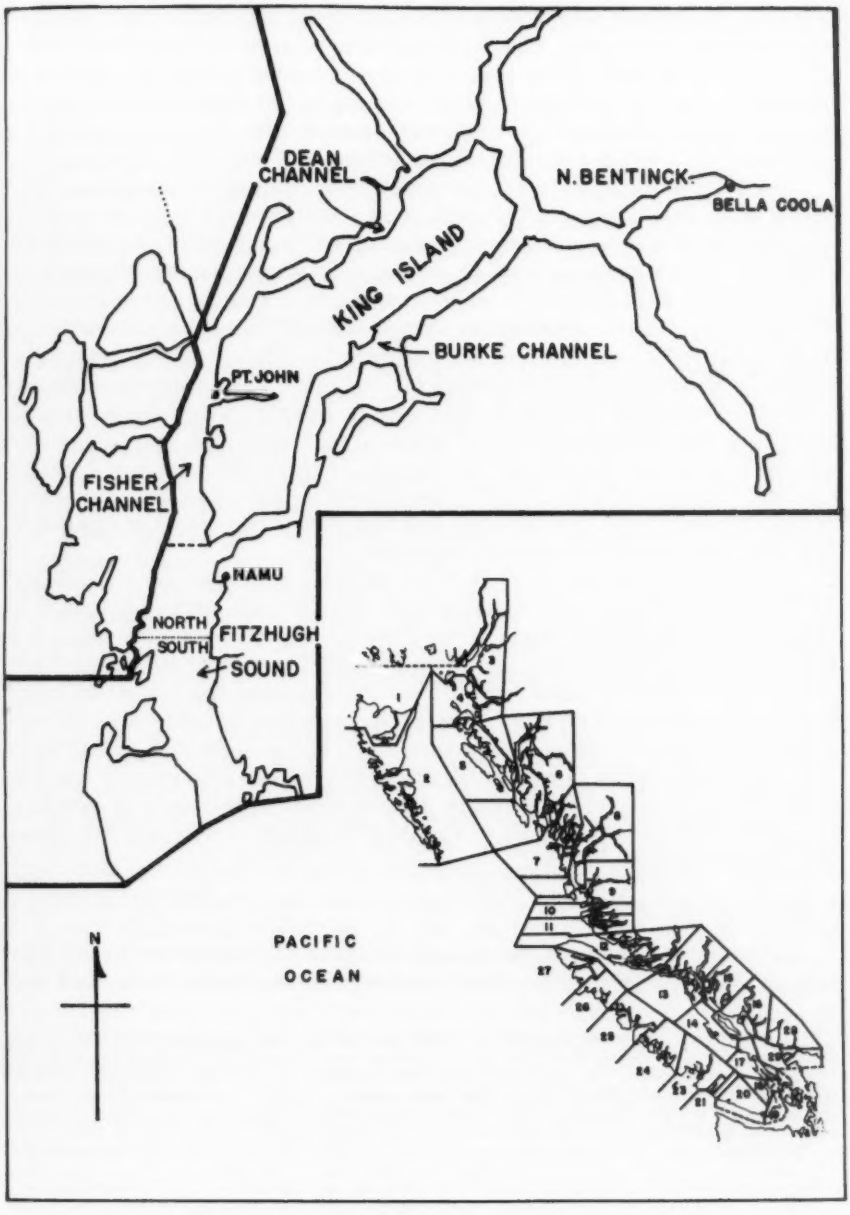

FIG. 5. A map of the coast of British Columbia showing the Statistical Commercial Fishery Areas, with an enlarged plan of Statistical Area 8.

fish were in fact the survivors of those artificially marked, rather than fish with naturally-missing fins. This point can be tested most directly by comparing the above figures with the incidence of missing fins of a type or combination not used in marking. Because no pinks were marked by removal of the adipose fin alone, the occurrence of such single marks provides an approximate *maximum* estimate of the incidence of naturally-occurring AdRV marks in the population.

Previous scattered studies have indicated that adipose fins can be naturally absent from Pacific salmon, but with great variation from stock to stock or from year to year. The greatest incidence reported is apparently by Pritchard (1939, p. 243), who discovered 12 missing adipose fins among a sample of 26,394 wild fry at McClinton Creek, Queen Charlotte Islands, or nearly 0.05%. The same investigator reported no missing adipose fins among 19,000 adult pinks at Tlell River, suggesting an incidence less than 0.005%. Among the 1,160,645 adult pink salmon examined in 1962 in the Central region of British Columbia (Statistical Areas 6–9) there were no fish that lacked the adipose fin alone. The best estimate of their incidence in this region and year is therefore something less than 1/1,160,645, or 0.0001%, with an upper limit of 0.0005% for 99% confidence (Ricker, 1937). The probability that both the adipose *and* the right ventral would be naturally absent is one or two orders of magnitude less than this, hence is completely negligible.

For the both-ventral (BV) marks a less direct comparison is available. In 1963, 18 BV marks were obtained from 504,639 pink salmon examined in catches from the Central region of the British Columbia coast. No young fish had been marked BV in 1962, so these 18 might have been either age-3 fish of the 1961 marking or age-2 fish with naturally missing fins.[3] In either event they can be used to set an *upper limit* for the probable frequency of occurrence of naturally-missing typical BV marks in 1963: 18 out of 504,639, or 0.0036%. The observed incidence of typical BV marks in 1962 was 5997 out of 1,160,645, or 0.516% — about 140 times greater than in 1963. Thus we can be sure that the great majority, possibly all, of the 1962 BV marks were in fact fish whose fins had been clipped in 1961.

Scale Examination

Scales were taken from the second row above the lateral line and slightly behind the dorsal fin. Scales from randomly-selected series of marked and

[3]Unfortunately no scales from these 18 fish are available. One possibility is that they were second-year fish on which both of the ventral fins had been attacked by chalimus larvae of the copepod *Caligus clemensi*. This parasite attacks the rayed fins (but not the adipose fin) of small salmon in the sea, and produces a scar that often appears "typical" — indistinguishable from a clipped fin (Parker and Margolis, 1964). Parker's unpublished observations show that *C. clemensi* were much more numerous on young salmon in Fitz Hugh Sound in 1962 than in 1961, 1963, or 1964. Usually only one fin on a fish is attacked by *Caligus*, but sometimes two are destroyed. The incidence of single ventral fins missing from adult fish in 1963 was much higher than that of both ventrals: 83 RV and 120 LV marks were found among the 504,639 pink salmon examined, although no single-ventral fins had been intentionally clipped and liberated in 1962 (a very few were mismarked in the course of removing both ventrals). Thus the 203 single-ventral marks of 1963 were all or almost all naturally-missing fins, probably destroyed by *Caligus*; and the 18 BV marks might have originated in the same manner.

unmarked fish were examined under a projector at a magnification of 100 diameters. The whole of the scale was examined carefully for checks. A band of narrowly-spaced circuli was invariably found in the position that has been regarded as the "regular" annulus. No definite additional checks of the type illustrated by Anas (1959) were found toward the margin from the annulus, but extra checks inside the presumed annulus were fairly common. These inner checks were subjectively classified into the categories "faint," "fair," or "good" (Fig. 2–4). Distance from the scale focus to the outside edge of this check was measured, as well as the distance to the outer edge of the annulus; also, the number of circuli to these positions was counted.

MARKED PINK SALMON

A total of 159 pink salmon scales from marked fish was examined. Of these, 72 were from fish with the adipose and right ventral fins missing, and 87 were from fish with both the ventral fins missing (and having "typical" scars).

Whereas the outer or "regular" checks on these scales were nearly all quite definite, the checks that occurred in the inner position varied greatly in distinctness. The three subjective categories used to describe them grade into each other and into the "no check" category. An indication of the difficulty of defining these rings is given by the results of an examination of the same scales, 159 in number, by three different scale-readers, all of them experienced. The number of scales with an inner check in the faint category or better was estimated as 34, 37, and 44%, respectively. Similarly, the differences between the categories faint, fair, and good depended on the judgment of the individual reader.

Among the 72 scales examined from the AdRV group, 3% had a good check on the inner field of the scale, 7% a fair check, 25% a faint check, and 65% no check. Among the 87 scales from the BV group, 1% had a good check on the inner field of the scale, 3% a fair check, 35% a faint check, and 61% no check (Table I). Combining the three categories of checks, 35% of the AdRV fish and 39% of the BV fish had an inner check. Figures 6–7 show the position of the inner or supplementary check, and of the outer check or annulus. The inner check occurred between the 7th and 18th circulus, and the distance from the focus to the outer edge of the narrowly-spaced circuli was 0.3–0.65 mm. The outer check occurred between the 21st and the 36th circulus, and was 0.75–1.2 mm from the focus. There was no overlap between the two types of check in these respects. The positions of both checks on the scale were consistent as between the BV and AdRV groups of marked fish.

If both inner and outer checks were to be considered as winter bands, then from 35 to 39% of the pinks in these samples would have spent two winters in the ocean and returned in their third year as maturing fish. But in fact these scales were from marked fish which are known to be in their second year of life.

Thus either the inner or the outer check observed on these scales must be accepted as the annulus and the other one as something other than an annulus. The usual interpretation has been to regard the outer check as the annulus

TABLE I. The frequency of occurrence of the supplementary check near the focus of scales of marked and unmarked pink salmon and marked chum salmon from the Bella Coola and adjacent regions, 1962.

	Pink salmon						Chum salmon	
Fins removed:	Both ventrals		Adipose right ventral		None		Both ventrals	
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Supplementary check								
None	53	61	47	65	67	67	2	14
Faint	30	35	18	25	22	22	5	36
Fair	3	3	5	7	10	10	6	43
Good	1	1	2	3	1	1	1	7
Total with check:	34	39	25	35	33	33	12	86
Total samples:	87	100	72	100	100	100	14	100

and the inner check as a supplementary check. The reasons for this choice are that the outer check is usually much more definite, and that it corresponds in position to the single check on scales which have only one. This is evident in the Figures. On scales which lack an inner check, the number of circuli to the outside edge of the annulus varies from 19 to 34, and the distance is 0.7–1.2 mm. On scales which have an inner check, the number of circuli to the outside edge of the outer check was 21–36, and the distance was 0.75–1.2 mm. This strongly suggests that the outer check, on scales having both an inner and outer check, is formed at the same time as is the single check on scales that lack an inner check, and is in fact the winter band or annulus.

UNMARKED BELLA COOLA PINK SALMON

For comparison with the marked pinks above, 100 scales from unmarked pink salmon caught by the commercial fishery in Fishery Area 8 in 1962 were selected randomly throughout the run and examined (Table I). Of these 100 fish, 67% had no check, and 33% had a supplementary check near the scale focus, including 22% faint checks, 10% fair, and 1% good. In the following year (1963) 395 fish were examined of which 80% had no check, 3% had faint checks, 8% fair, and 8% good.

The supplementary check on the 1962 scales occurred between the 5th and 14th circulus and was 0.25–0.5 mm distant from the focus (Fig. 8).

The similarity between marked and unmarked pinks in respect to position and incidence of supplementary checks suggests they were formed at about the

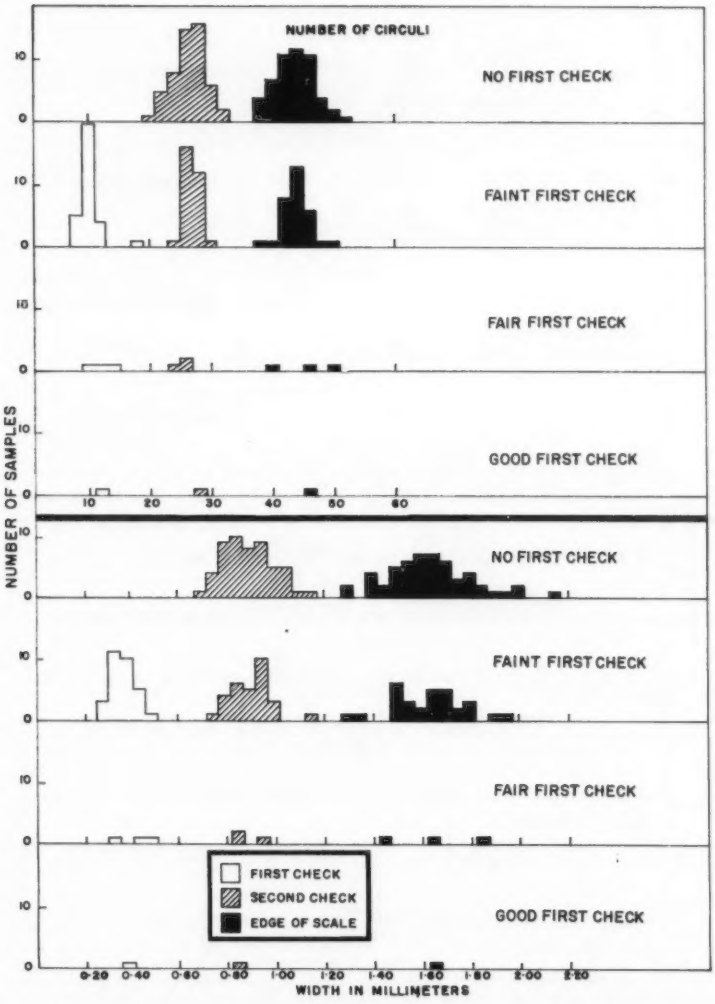

FIG. 6. Scales taken in 1962 from pink salmon that were marked by removal of both ventral fins at Hook Nose Creek in 1961. *Above*: Number of circuli to the first (or supplementary) check, to the second check, and to the scale margin. *Below*: Distance in millimetres to the first check, second check, and margin.

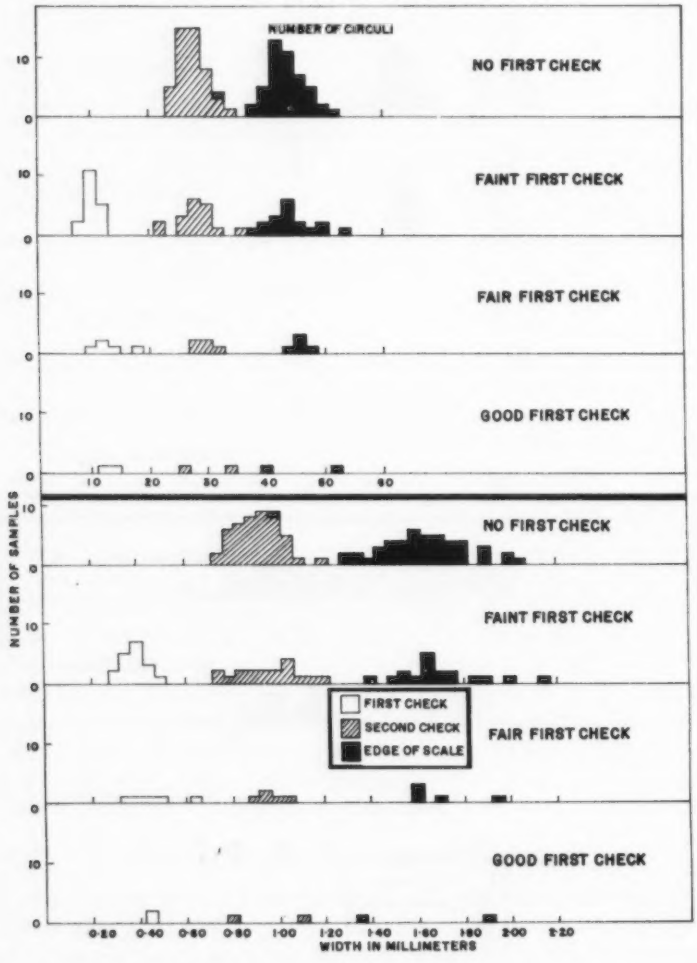

FIG. 7. Scales taken in 1962 from pink salmon that were marked by removal of the adipose and right ventral fins at Fisher Channel in 1961. *Above*: Number of circuli to the first (or supplementary) check, to the second check, and to the scale margin. *Below*: Distance in millimetres to the first check, second check, and margin.

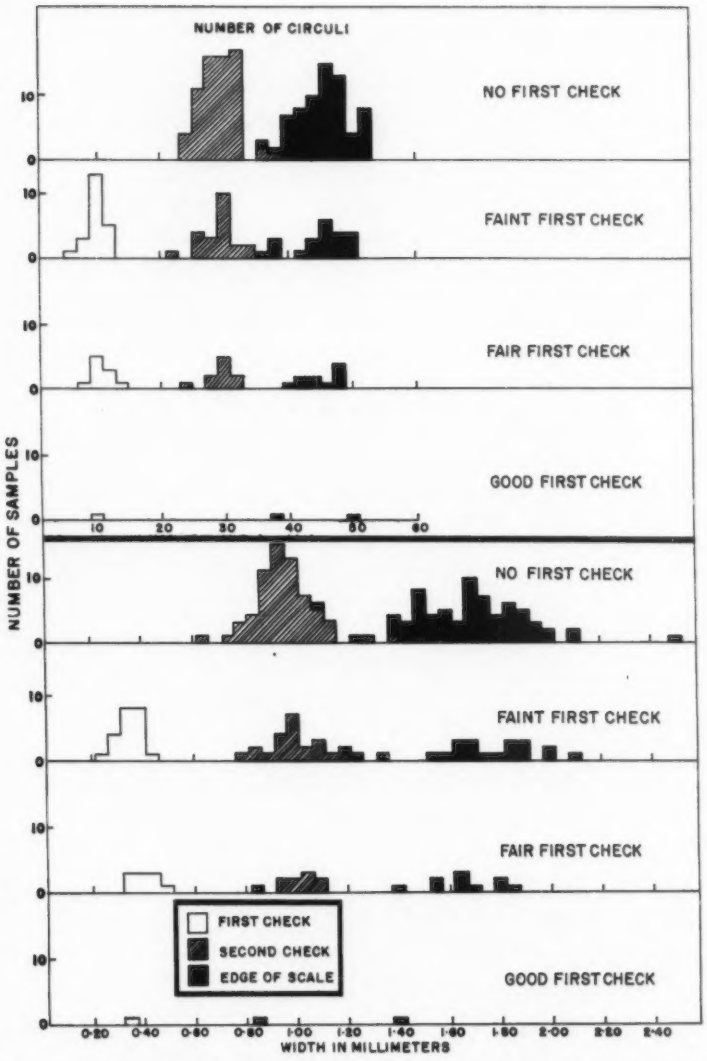

FIG. 8. Scales taken in 1962 from unmarked pink salmon caught in the Bella Coola fishery area. *Above*: Number of circuli to the first (or supplementary) check, to the second check, and to the scale margin. *Below*: Distance in millimetres to the first check, second check, and margin.

same time among both types, possibly associated with some change in the food supply or in the physical environment. There is no suggestion that the supplementary check on the scales of the marked pinks was associated with effects of marking or the absence of the fins.

FRASER RIVER PINK SALMON

The pink salmon of the Fraser River and adjacent streams exhibit extreme disparity in abundance between the dominant odd-numbered years and the "off" even-numbered years. The ratio of the catches in odd and even years is typically of the order of 1000:1. With such disparity, any small percentage of age-3 spawners among broods hatched from odd-year spawnings would mean a large percentage of age-3 fish present in the even-year runs. In fact, even if all even-year fish were 3 years old, the incidence of age-3 fish produced by the odd-year spawners would average only about 1 in 1000 or 0.1%.

Scale samples from pinks of the Fraser region (Statistical Area 29) were examined in the same way as the Bella Coola fish. Samples for 5 odd-numbered years and 1 even-numbered year were available (Table II).

The most revealing information in Table II is the fact that the odd-year pinks contained rather large numbers (20–60%) of supplementary rings. In most years these included some checks classified as "good" — the incidence of the latter varied from 0 to 11%. Comparing the size of the stocks as indicated by weight caught (last column of Table II), it is obvious that the feeble even-

TABLE II. Incidence of supplementary checks in Fraser River pink salmon, and catches from runs to the region of the Fraser River and certain adjacent regions (Statistical Areas 19, 20, 21, 23, and 29).

Year	Supplementary checks				Total checks	Total scales	Per cent with checks	Catch (thousands of pounds)
	None	Faint	Fair	Good				
1955	64	..	..	..	46[a]	110	42	25,857
1956	..	..	..	..	..	..	..	17
1957	18	8	5	0	13	31	42	14,390
1958	3	2	4	0	6	9	67	25
1959	39	33	15	11	59	98	60	11,296
1960	..	..	..	..	..	..	..	10
1961	70	23	8	5	36	106	34	3,465
1962	..	..	..	..	..	..	..	29
1963	144	42	10	10	62	206	20	21,568

[a]Checks for 1955 fish were not classified.

FIG. 9. Scale from a marked adult chum salmon (4_1), showing the absence of a supplementary check and the winter checks (B), (C), (D).

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FIG. 10. Scale from a marked adult chum salmon (4_1), showing a supplementary check (A) and the three annuli (B), (C), (D).

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year populations could not possibly have produced the observed 20–60% of odd-year fish with supplementary checks, or even just the 5–11% with good supplementary checks observed in 3 of the 4 years. Hence, even without marking experiments we may be sure that in the Fraser pink stock the supplementary checks are not true annuli.

Six of the nine 1958 fish had supplementary rings, a value not significantly higher than some of the figures for odd-numbered years. Hence even the few even-year pinks present cannot be regarded as third-year fish on this evidence. None of these nine had a scale pattern resembling the pink salmon plausibly interpreted as age 3 and figured by Anas (1959).

BELLA COOLA CHUM SALMON

In 1961, Dr Parker and his staff also marked a large number of seaward-migrating chum salmon fry of the 1960 brood year at Hook Nose Creek, by removal of both ventral fins (BV). No special effort was made to recover these marked fish during the first 2 years they were expected in the fishery (1963 and 1964). However in 1964, as part of a routine sampling of salmon catches for size and age studies, 14 BV-marked chum salmon were recovered in the central part of the British Columbia coast.

The scales of these 14 double-fin marked chums were examined for age and for the occurrence of a supplementary check near the focus of the scale (Fig.

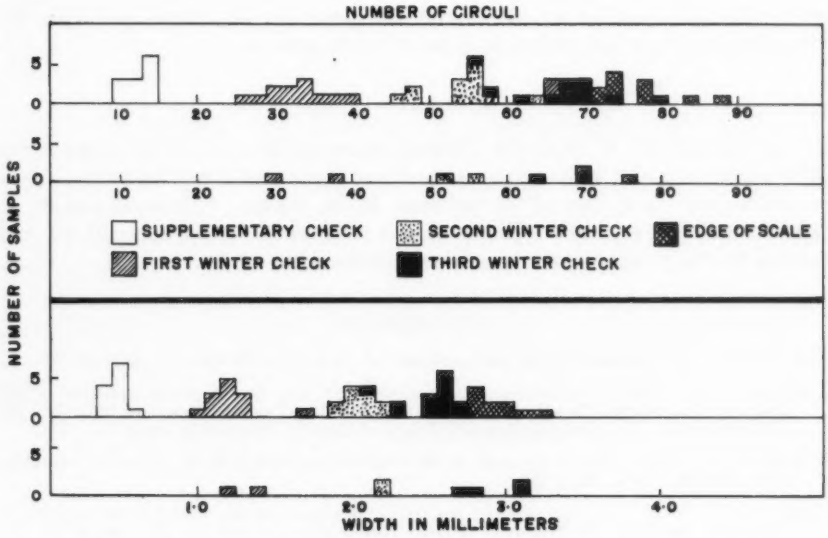

FIG. 11. Scales taken in 1964 from chum salmon that were marked by removal of both ventral fins at Hook Nose Creek in 1961. *Above*: Number of circuli to the supplementary check, to the winter checks, and to the scale margin. *Below*: Distance in millimetres to the same.

9–10). All 14 scales from the marked fish had three clear checks that were interpreted as winter bands or annuli; thus they were classified as 4-year-olds from the 1960 brood year, which is in agreement with their having been marked in 1961. Twelve of the 14 scales (86%) from the marked fish also had a supplementary check near the focus of the scale: in 7% the check was classified as good, 43% were fair, 36% were faint, while 14% had no check at all (Table I). The supplementary check occurred between the 9th and 14th circulus from the focus and the distance from the focus to the outer edge of the check was 0.4–0.6 mm (Fig. 11). The check regarded as the first annulus on these scales occurred between the 25th and 40th circulus and was 1.0–1.3 mm from the focus. There was no overlap between the two types of check. The supplementary check on the scales from the marked chum salmon occurred at about the same relative distance from the focus of the scale as did the supplementary check on the scales of the marked pink salmon, having regard to the larger size of chum scales.

CONCLUSION

The scales of double-fin marked pink and chum salmon of known age support the prevailing view that the check which is often found near the focus of pink and chum salmon scales is not a winter band but is a supplementary check. Unmarked pink salmon had the same incidence and degree of distinctness of supplementary checks as the marked ones.

The biological interpretation of the supplementary check is uncertain, but it may correspond to some change in the physical environment of food supply during the first year of sea life of the fish, perhaps just before or during the time they leave coastal waters and move to the open sea.

ACKNOWLEDGMENTS

It was Dr R. R. Parker's marking experiments that made possible the direct comparison of scale structure and age reported here. The authors wish to extend thanks to Drs M. P. Shepard, R. R. Parker, F. Neave, and P. A. Larkin who have read the manuscript and made constructive suggestions, and to Mrs M. Aarts who made the measurements of the scales.

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The Relation of Size to Rate of Oxygen Consumption and Sustained Swimming Speed of Sockeye Salmon (*Oncorhynchus nerka*)[1,2]

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ABSTRACT

The relation of size (log weight, g) to metabolic rate (log O_2-uptake, mg O_2/hr) of sockeye salmon was found to have a continuous change in slope (0.78–0.97) with increasing activity at 15 C.

The slope of the equation relating the 60-min sustained swimming speed (log speed, cm/sec) to length (cm) had a value of 0.50, demonstrating a rapid decrease in relative performance with increasing size.

INTRODUCTION

The relation of weight to metabolic rate of fish has received considerable attention, particularly for resting or standard rates of metabolism (Winberg, 1956, 1961; Fry, 1957). Relatively few experiments have dealt with the influence of weight on active metabolism (Job, 1955; Basu, 1959). Intermediate levels of metabolic rate, generally designated as routine metabolism, have been investigated in a number of cases (Job, 1957; Beamish and Mookherjii, 1964; Beamish, 1964) but the level of activity is hard to standardize or relate to any discrete behaviour pattern.

It has been the aim of current studies on the metabolic rate of sockeye salmon (*Oncorhynchus nerka*) to determine the energy required to swim at any fixed speed, and to assess the separate effects of temperature and size (Brett, 1962). Experiments on 50-g yearling sockeye at acclimation temperatures ranging from 5 to 24 C have been conducted (Brett, 1964). Further experiments are reported herewith on the metabolic rates of sockeye salmon ranging in weight from approximately 3 to 1400 g, performed at 15 C in fresh water.

MATERIALS AND METHODS

A description of the tunnel-respirometer and the method of operation has been presented (Brett, 1964).

In brief, fish are forced to swim in front of an electrically charged screen (3–5 v a-c) in a plexiglass tube 11.4 cm (4½ inches) in diameter. The tube is expansible to any desired length by the addition of new sections (Fig. 1). A centrifugal pump recirculates the water past the fish at velocities up to 113

[1]Received for publication April 23, 1965.
[2]Paper No. 14 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada Biological Station, Nanaimo, B. C.

J. Fish. Res. Bd. Canada, 22(6), 1965.
Printed in Canada.

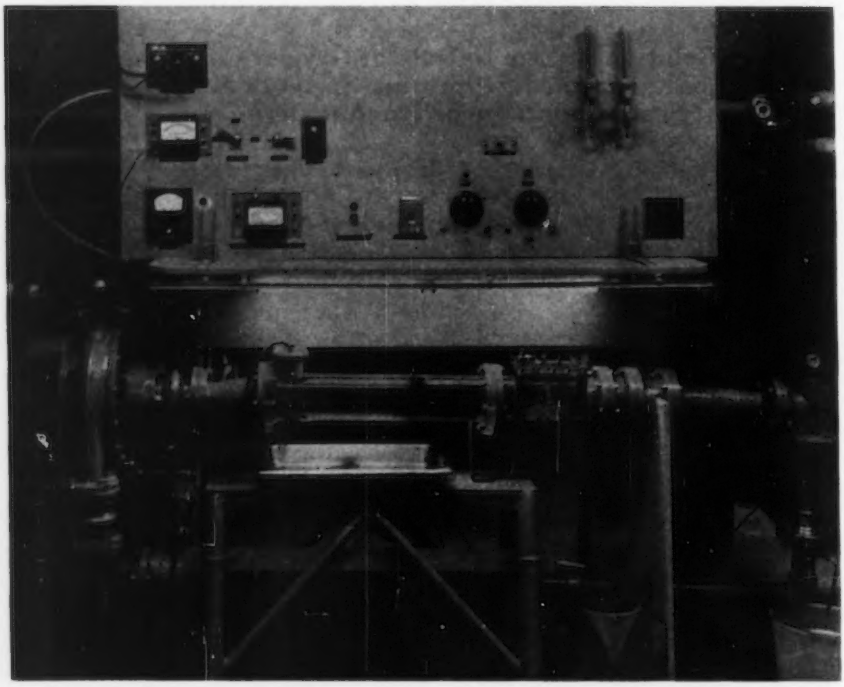

FIG. 1. Tunnel-respirometer with expanded plexiglass chamber providing a volume of 23.41 (7.0 gal).

cm/sec (3.7 ft/sec). New water can be exchanged at will without altering the internal flow pattern.

Each fish, or group of fish, is put through a set procedure including 36 hr of fasting and 14 hr of conditioning in the respirometer prior to the start of a test. Commencing at a low velocity, oxygen consumption rates are determined (unmodified Winkler) for two 30-min periods, followed by flushing to re-establish the oxygen level. The velocity is then increased by 9.1 cm/sec (0.3 ft/sec) and determinations repeated. This step-type procedure is continued until a fatigue velocity is reached.

Active metabolism is determined directly for the maximum sustained speed; standard metabolic rate is obtained by extrapolating the *O_2-consumption* versus *velocity* curve back to zero velocity.

With the exception of the adult salmon all samples were from cultured stocks (Table I). The adults were obtained by trapping early-run sockeye a few days after entering Stamp River, Vancouver Island, B. C. They were held in fresh water for 3 weeks prior to testing. Although fish heavier than 1400 g were available these could not swim readily in the relatively small diameter of the fish chamber.

TABLE I. Metabolic rates and corresponding swimming speeds of sockeye salmon tested at 15 C.

Class		Age	Sex	Total length	Wet weight	Oxygen consumption (mg O_2/kg/hr)							Swimming speeds (60-min duration)							
						Min observ	Max observ	Standard	¼ Active	½ Active	¾ Active	Full Active	¼ Active		½ Active		¾ Active		Fatigue speed	
		(yr)		(cm)	(g)								(cm/s)	(L/s)	(cm/s)	(L/s)	(cm/s)	(L/s)	(cm/s)	(L/s)
Underyearling	(No.)	..	..	(10)[a]	(10)	..	(1)[b]	(1)	..	..	..	(1)	..	..	..	..	..	..	(1)	(1)
	Mean	0.3	Imm.	7.74	3.38	..	635	230	330	460	660	920	12.8	1.66	25.7	3.32	38.5	4.98	51.5	6.65
	S.E.	..	..	.06	.10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Underyearling	(No.)	..	..	(9)	(9)	..	(2)	(2)	..	..	..	(2)	..	..	..	..	..	..	(9)	(9)
	Mean	0.7	Imm.	10.03	8.47	..	860	110	185	300	515	830	15.0	1.50	30.0	3.00	45.0	4.50	59.8	5.94
	S.E.	..	..	0.17	0.46	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.17
Underyearling	(No.)	..	..	(42)	(42)	..	(7)	(7)	..	..	..	(7)	..	..	..	..	..	..	(7)	(7)
	Mean	0.9	Imm.	12.78	19.1	..	655	127	..	..	..	700	..	..	..	..	..	..	53.2	4.16[c]
	S.E.	..	..	0.21	1.6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.23
Yearling	(No.)	..	..	(10)	(10)	(7)	(8)	(10)	..	..	..	(8)	..	..	..	..	..	..	(8)	(8)
	Mean	1.4	Imm.	18.8	55.2	121	988	71	132	250	480	895	19.4	1.03	38.7	2.06	58.1	3.09	77.4	4.12
	S.E.	..	..	0.8	9.5	..	..	4.0	..	..	..	49	..	..	..	..	..	..	3.6	0.19
Adult (jacks)	(No.)	..	..	(4)	(4)	(4)	(4)	(4)	..	..	..	(4)	..	..	..	..	..	..	(4)	(4)
	Mean	3.4	♂	41.8	746	93	708	71	126	226	410	730	31.7	0.75	62.7	1.5	94.1	2.25	125	3.0[d]
	S.E.	..	..	1.13	8.9	..	..	3.9	..	..	..	45	..	..	..	..	..	..	..	..
Adult	(No.)	..	..	(14)	(15)	(9)	(12)	(5)	..	..	..	(9)	..	..	..	..	..	..	..	..
	Mean	4.4	♀[e]	53.9	1432	150	658	44	88	176	350	717	35.5	0.66	71.5	1.33	107	1.99	143	2.65[f]
	S.E.	..	..	0.67	40.6	..	..	5.6	..	..	..	25	..	..	..	..	..	..	..	..

[a,b] Total number of fish tested; number of groups within total.
[c] This performance significantly low from lack of pre-exercise and tested in fall (see Fig. 3).
[d] Determined by interpolation, Fig. 3.
[e] These adults were 80% 4_2 and 93% females.
[f] Determined in an 11-inch diameter tunnel at 17 C.

When swimming in a closed system the cross-sectional displacement of water by the fish naturally influences the velocity over the body. Since the displacement was less than 10% at the greatest body cross-section of the yearling fish no correction was applied. Adult fish, however, with relatively large mid-section, and consequently impeded by the increased surface drag, could not obtain more than half their normal swimming speed. That they were working hard was revealed by the observation that a tail-beat frequency of about 180–200 beats/min characterized the threshold level of sustained effort. This frequency was also the maximum sustained rate when tested in an 11-inch diameter tunnel at nearly twice the velocity.

It was therefore possible to use tail-beat frequency instead of velocity for the larger fish in order to determine the relation of oxygen consumption to intermediate levels of activity. It also made it possible to impose fatigue velocities on large fish to establish the maximum rate of oxygen uptake, despite the limitations of the small respirometer.

RESULTS

The results for each weight "class" are compiled in Table I, with metabolic rates expressed in terms of unit wet weight (1 kg). Minimum and maximum observed rates are included wherever appropriate; few cases were studied at sufficiently low velocities to warrant including many "resting" rates. Underyearling fish were tested in groups of 4–10 fish at a time, as signified in the "Numbers" column.

The smallest fish (3.38 g) had standard and active metabolic rates of 230 and 920 mg O_2/kg/hr, whereas the largest (1432 g) had rates of 44 and 717 mg O_2/kg/hr, respectively.

The values for intermediate levels of activity corresponding to $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the 60-min sustained swimming speed, were obtained by interpolation from the *O_2-consumption* vs *velocity* curves (Fig. 2).

The maximum 60-min sustained swimming speeds (Table I) ranged from 51.5 cm/sec (1.7 ft/sec) for the shortest fish (7.74 cm total length) to 143 cm/sec (4.7 ft/sec) for the longest (53.9 cm). When expressed in terms of length/sec these speeds beçome 6.65 and 2.65 L/sec, indicating the reduction in *relative* speed which characterizes the larger fish (Fig. 3).

The sustained speed of the 12.8-cm underyearling fish has not been used in defining the speed–length relation. These fish were not pre-exercised. They were relatively fat, and were tested in the fall. These factors are sufficient to cause significant differences in performance (Wohlschlag and Juliano, 1959).

DISCUSSION

The use of groups of small fish rather than individuals was two-fold. Single, small fish in the 23-liter volume of the respirometer had too small an influence on the oxygen concentration to make $\frac{1}{2}$-hr readings feasible. In addition, the time to test individual fish (1 day) was too long for amassing comparative data.

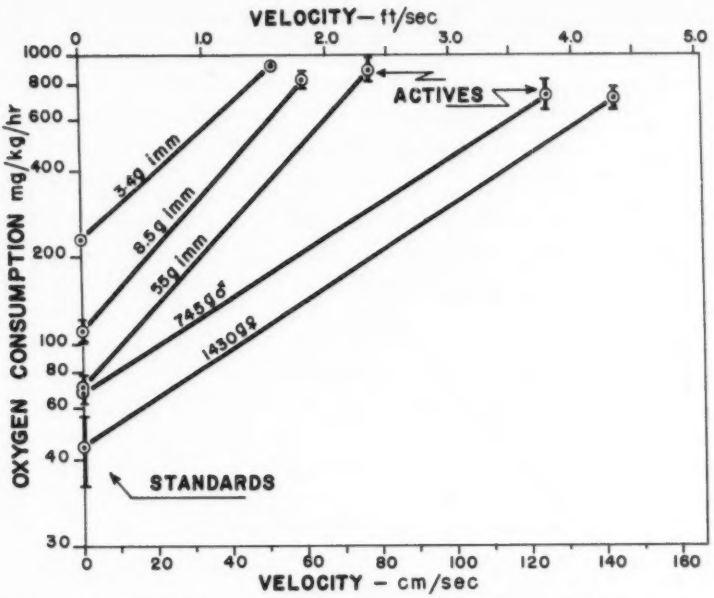

FIG. 2. Standard and active metabolic rates with corresponding 60-min maximum sustained swimming speeds for five weight "classes."

The question arises whether grouped fish give different metabolic rates than single fish. While this forms the basis of another study it can be reported that no difference is as yet apparent under the conditions of conducting experiments with swimming fish. Variability is reduced indicating the averaging effect of a group response but also, possibly, of a reduction in restless behaviour and general excitement. For the present, the data on weight influence have been considered to be unaffected by any group factor.

The general equation relating metabolic rate (Y, mg O_2/hr) to weight (X, g) has been expressed in the form $Y = aX^b$, or $\log Y = \log a + b \log X$. Applying this transformation to the data of Table I and using the method of least squares[3] to determine the equations for standard and active metabolic rates, the slope values for b, the rate of change of metabolic rate with size can be computed (Table II, Fig. 4). A moderately fan-shaped set of lines is obtained.

STANDARD METABOLIC RATE

If all the data for standard metabolism are treated together a b-value of 0.775 ± 0.145 results (Table II). This serves to link all the observations and would appear to be best for purposes of extrapolating to weights greater than

[3]Individual points for all fish could not be used since some determinations were for groups. The means have been treated therefore as points of equal statistical weight.

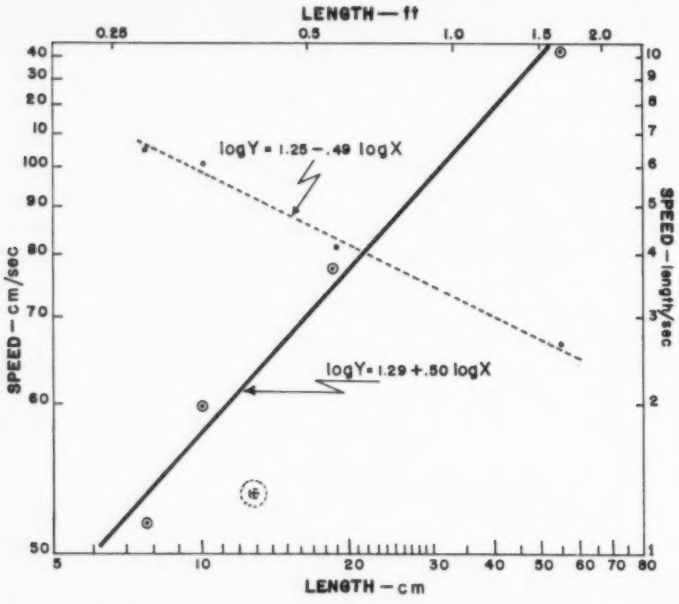

FIG. 3. Relation between 60-min maximum sustained swimming speed and total length. Speed expressed as cm/sec for solid line, and as length/sec (L/sec) for broken line. Circled point is for mean speed of the underyearling fish (12.8 cm) which were not pre-exercised and were tested in October (see text).

1400 g. However, between the yearling and adult stages in fresh water a period of rapid growth characterizes sea life. A change in metabolic slope may well accompany this phase. If the early freshwater period is treated separately a *b*-value of 0.624 results, a significant reduction in this parameter. Just as stanzas are found in growth rate it is not unlikely that similar sorts of stanzas may characterize the rate of change of metabolic rate.

There is also a sex factor entering into the mature stage. Here, too, differences may exist as suggested by the dotted lines in Fig. 4. During maturation the gonad of the female has from two to five times the relative weight of that of the male (Idler and Clemens, 1959).

Attention is drawn to these points in order to show the potential limitations of pooled treatment of the data, at least where standard metabolism is concerned. So much has been written on the significance and interpretation of *b*-values since the "surface law" propounded for homeotherms over a century ago, which requires a value of $\frac{2}{3}$ or 0.67 (Bertalanffy, 1957, 1964; Kleiber, 1961) that it is not hard to make interpretive comparisons which, with closer study, may turn out to be unjustified. Although Winberg (1956) examined 266 cases for freshwater fish and was able to provide an average value of $b = 0.81$ (20 C), Heusner *et al.* (1963) in a critical study of three species (*Lebistes reticulatus*, *Xiphophorus helleri*, and *Aequidens latifrons*) at 25 C obtained mean slope

TABLE II. Equations for relation between metabolic rate (Y, mg O_2/hr) and weight (X, g) at different levels of activity expressed as fractions of the maximum 60-min sustained swimming speeds. Confidence limits of slopes given for $p = 05$.

Activity level	Equation	Limits
0 = Standard (total)	$\log Y = -0.632 + 0.775 \log X$	± 0.145
0 = Standard (immature)	$\log Y = -0.491 + 0.624 \log X$	..
¼ Max	$\log Y = -0.523 + 0.846 \log X$	..
½ Max	$\log Y = -0.357 + 0.890 \log X$	..
¾ Max	$\log Y = -0.223 + 0.926 \log X$	..
Max = Active ($n = 6$)	$\log Y = -0.050 + 0.970 \log X$	± 0.053
Active ($n = 5$)[a]	$\log Y = -0.064 + 0.963 \log X$	± 0.012

[a] If the active metabolic rate of the 12.8-g fish tested in the fall is eliminated, a slightly reduced slope and reduced error result.

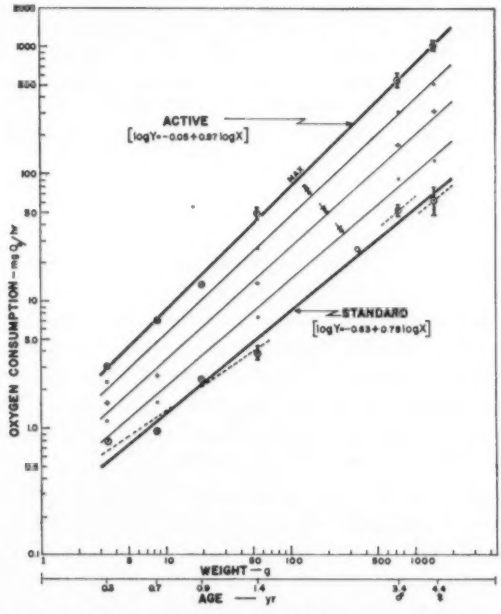

FIG. 4. Relation between metabolic rate and weight for different levels of activity expressed as fractions of the maximum 60-min sustained speed (max). Experiments performed in fresh water at 15 C. Broken lines represent possible relation of standard metabolism for immature freshwater stage, and for mature fish of different sex. Wherever fish were tested singly limits of ±2 S.E. are indicated.

values of 0.70, 0.78, and 0.70 (overall mean = 0.73). By contrast Beamish (1964) and Beamish and Mookherjii (1964) report *b*-values of 0.88 for *Salmo trutta*, 1.05 for *Salvelinus fontinalis*, 0.86 for *Catostomus commersonii*, 0.93 for *Ictalurus nebulosus*, 0.89 for *Cyprinus carpio*, and 0.85 for *Carassius auratus* (overall mean = 0.91). With such a range of difference, varying all the way from near surface proportionality (0.67) to direct weight proportionality (1.00) the value of applying a generalized relation is questionable.

Since standard metabolism relates to the maintenance costs of a non-feeding, nondigesting, nongrowing, nonactive fish there is reason for Winberg's (1956) appeal for increased studies on active metabolism — ". . . there is no need for additional accumulation of data on metabolic rate of fish under conditions of weak activity or nearly resting, because not one of the basic problems of theoretical or practical interest can be solved in that manner." In medical research Drabkin (1959) makes a similar plea — "Recognition of the large variations in overall metabolic rate encountered in the customary non-basal states of the normal living body has made it necessary to refer measurements in the metabolic clinic to a more reproducible base line [than basal metabolic rate]; the BMR values . . . have tended to steer us away from the factor of performance capacity, which should be of major interest to the biologist and clinician." Drabkin further proposes an *index of metabolic expansibility*, defined as the ratio of metabolic capacity (in prolonged muscular work or at peak effort) to basal metabolism (Drabkin, 1950, 1959). This index, proposed for mammalian studies, is similar in concept to Fry's derived *metabolic scope* for fish (Fry, 1947).

Active Metabolic Rate

The determination of active metabolic rates is not subject to certain of the factors contributing to the variability of standard metabolic rates. The effect of excitability and spontaneous movements are virtually eliminated for active metabolic rate. What is more, the latter has a magnitude which is not affected proportionally as much by small changes. The closeness of fit of the data for active metabolism supports this contention (Fig. 4). The animal must, however, be pressed to maximum performance, otherwise behavioural problems may occur which limit full metabolic expression.

Of considerable interest is the progressive increase in slope with increasing activity (Table II). Starting at 0.78 for resting state the slope rises to 0.97 for maximum sustained performance. Since a large proportion of the body of a fish is muscle the almost direct weight relation for active metabolism might be anticipated. The increase between 0 and $\frac{1}{4}$ activity is 0.07. This small increment probably accounts for the similarity of slopes (within one species) for standard and routine rates.

In contrast to the phenomenon of increasing slope values in the salmon, a decreasing slope relation characterized the relation of metabolic rate to weight for increasing work load in mice (Bertalanffy, 1964). The great difference in

the problem of dissipating heat between a water-breathing poikilotherm and an air-breathing homeotherm undoubtedly accounts for major differences in slope relations for active metabolic rates.

Turning to temperature relations Job (1955) found for *Salvelinus fontinalis* that the slope value b at 5 C for active metabolic rate (0.94) was higher than for standard (0.86). At 15 C, however, the slopes were the same; whereas at 20 C the relation was reversed, the standards having a slope of 0.80 and the actives 0.75.

In the interests of accurate prediction of metabolic rate the need to establish the particular weight relation for the species concerned at the temperature and level of activity anticipated appears to be inescapable.

Active/Standard Ratio

If the *metabolic expansibility* index is determined it can be seen that a great difference exists between the lowest value of 4.0 for the smallest fish and 16.3 for the largest (Fig. 5). Although considerable variability exists, affected by such factors as pre-exercise, maturity, and sex, the basic influence of size can best be displayed by obtaining the Active/Standard ratios from the lines-of-best-fit relating metabolic rate and weight (Fig. 4). The progressive decrease

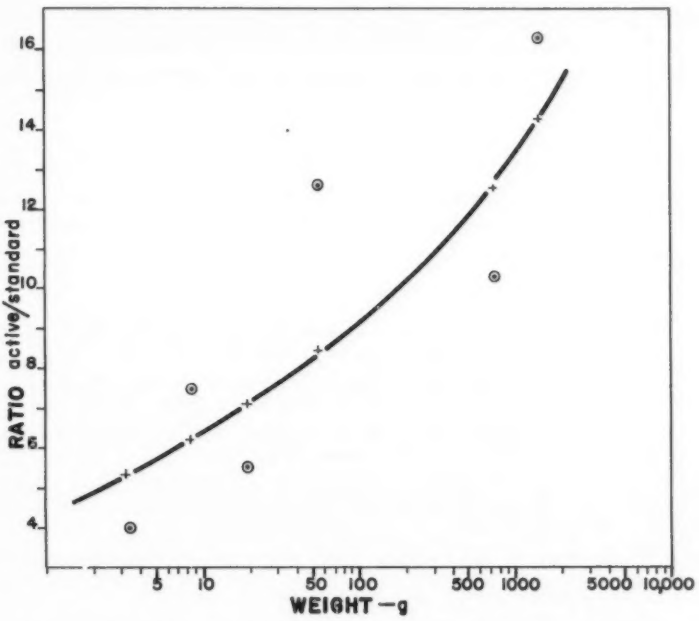

FIG. 5. The ratio of active to standard metabolic rate (metabolic expansibility) in relation to weight. Circled points are from observed mean metabolic rates; small crosses are derived from the lines of best fit, Fig. 4.

in standard metabolism with size, when related to a fairly sustained active metabolic rate, provides an increased metabolic scope.

Performance Relations

At the highest sustained level of performance the muscular demand for oxygen is met by the maximum rate of oxygen uptake. Burst speeds invoke oxygen-debt and fatigue.

The 60-min maximum sustained speed is considered here, determined as the final step in a performance sequence lasting 5–7 hr. This has been shown to approximate threshold levels of performance in tests where fixed velocities were imposed for up to 10 hr (Brett, 1964). Much of the work on swimming speed reported in the literature has been on measures of burst speeds (Bainbridge, 1960, 1962; Boyar, 1961).

The relation between body length and swimming speed (Fig. 3) follows the general equation $Y = aX^b$ where Y is swimming speed (cm/sec) and X is total length (cm). Alternatively speed has been expressed in total fish lengths/sec (L/sec). In either case the slope b approximates 0.5 indicating a rapid decay in the *relative ability* to maintain a sustained speed as size increases.

This decay occurs despite a relative increase in body musculature (45% for 30 g; 60% for 1500 g) and a progressive increase in metabolic scope. Even with these assets it is apparent that the increased hydrodynamic drag which accompanies increased size is only partially met. The metabolic process is not a match for the great energy cost of sustained high speed for large fish.

Acknowledgments

Throughout the study the technical assistance of Mr D. B. Sutherland has contributed greatly to expediting the research. In addition it is a pleasure to acknowledge the assistance of Dr L. S. Smith in the determination of metabolic rates of adult salmon.

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Effect of Retention of Spermatozoa and Ova of Sockeye Salmon, *Oncorhynchus nerka*, in Water and Without Addition of Water, on Fertility[1]

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ABSTRACT

Viability of ova and of spermatozoa was retained after considerable exposure to water and to air before fertilization. Fertilization occurred when spermatozoa were held in water for 8 hr (10.9% ova fertilized) and in air for 72 hr (4.4%), and when ova were held in water for 28 min (3.4%) and in air for 96 hr (73.7%). Great variation in results suggested that little importance could be attached to the actual percentage of eggs fertilized.

In the course of an investigation of the propagation of sockeye salmon, *Oncorhynchus nerka*, at Cultus Lake, British Columbia (1925–38) (Foerster, 1938), experiments were undertaken from time to time to throw light on certain phases of propagation where pertinent information seemed desirable.

One of these was the period of fertilizability of both ova and spermatozoa after being removed, by hand stripping, from the ripe fish. It was of interest to know how long a sample of milt or of eggs could be held (a) in water and (b) in a "dry" condition, i.e., before addition of water, and still be capable of fertilization. The "in water" findings are of significance in the case of natural spawning, particularly to indicate the possibilities of eggs, deposited by a female not attended by a male, being fertilized by "stray" spermatozoa from adjacent spawning activities; they may indicate also, for artificial propagation, how long the spermatozoa remain active after water has been added to the spawning pans into which ova and milt are expressed from the fish being stripped. The "dry" findings may suggest how long eggs and milt, after being expressed from the ripe fish, may be held or may be transported elsewhere before being mixed with the other sex product, and still result in satisfactory fertilization.

METHODS

The experiments were conducted at the Department of Fisheries of Canada salmon hatchery at Cultus Lake during the normal autumn stripping operations. Samples of eggs and milt were taken from the normal stock of mature sockeye being held for stripping below the weir in Sweltzer Creek, the outlet stream from Cultus Lake. The initial experiments were commenced in 1925 but others followed in 1926, 1928, 1929, and 1931, each year the periods of retention of

[1]Received for publication February 24, 1965.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

ova and spermatozoa before fertilization being extended as suggested by the results for the previous year. In some instances earlier tests were also repeated.

PROCEDURES. Into each of a number of pint (500 cc) jars was put either a small quantity of ova (300–1000) or of milt (approximately 5 cc). Due care was taken, by wiping off the fish with a towel, to assure that no extraneous water fell into the egg and milt samples. For the tests of retention in water, each jar was then half filled with clean, fresh water, taken directly from a hatchery trough. The hatchery water supply came from a nearby creek which drained the adjacent partially-wooded hillside. The flow, thus chiefly run-off water, was exceedingly variable in quantity. Unfortunately no data are available on its chemical or mineral quality. At certain intervals the opposite freshly-taken sex product was added, the mixture allowed to set for a few minutes, then the "milky" liquid drained off. For the tests of retention in a "dry" state, i.e. without added water, the jars of ova or milt were held for certain intervals and then the opposite, freshly-taken sex product added, the mixture well stirred, the jars then half filled with fresh water, again carefully stirred and allowed to set for a few minutes. The water was then carefully drained off, all traces of extraneous milt and foreign matter flushed out, fresh water added, and the ova allowed to "harden."

When hardened, the ova in each jar were placed in lacquered trays and set in the hatchery troughs to incubate. In the hatchery the ova were inspected daily and all infertile eggs removed and counted. When development had reached the "eyed" stage the number of healthy ova remaining was ascertained. Water temperatures throughout the period fluctuated about a mean of 5 C (2–8 C).

While it was not at all difficult to obtain fresh, unstripped mature females for samples of ova, the collection of milt from the males was a different problem. Male fish were being stripped by the hatchery personnel in the course of the regular spawning operations and were, after being used, thrown back into the retaining pens or pools for subsequent use. When collecting milt, then, for the experiments here reported there could be no assurance that partly-spent or almost wholly-spent males were not utilized, though every precaution was taken to use what appeared to be males in good spawning condition. In some years the tests were conducted toward the end of the spawning season when adequate material was difficult to procure. Thus there was never any assurance that milt of good potency was being used.

RESULTS AND DISCUSSION

RETENTION IN WATER. Rutter (1902) for chinook salmon, *O. tshawytscha*, and Gray (1919) for Atlantic salmon, *Salmo salar*, have indicated that, within 2 min of their introduction into an aqueous solution, the spermatozoa lost the greater part of their motility and became inactive. The fertilizing period for spermatozoa is thus considered to be distinctly limited. Furthermore, Shuman (1950), in tests with pink salmon, *O. gorbuscha*, in which samples of ova were exposed to "clouds" of milt drifting downstream specific distances (up to 20 ft,

equivalent to 30 sec in the water) from where milt was manually expressed from ripe males, obtained the following results:

Distance (ft) of introduction of sperms from eggs	Time (sec) of drift of milt downstream to eggs	Number of eggs in samples	Percentage of eggs fertilized
1	1.5	12,950	78.7
2	3.0	12,740	66.6
4	6.0	11,550	58.8
10	15.0	13,090	17.9
20	30.0	10,535	4.8

On the other hand, Smirnov (1963) for *O. gorbuscha* of Sakhalin Island, records per cent fertilizations of 70 and 65 in two tests of ova treated with milt which had been held in water for 20 sec prior to application to the eggs; 54 and 29 where milt had been held in water for 30 sec; 2 and 3 where milt had been held in water for 140 sec.

The data obtained from the Cultus Lake experiments (Table I) do not provide, for spermatozoa held in water for varying intervals of time, the pronounced rapidly-decreasing trend in fertilizing ability with increase of retention period, as shown by Rutter and by Shuman, except in the 1934 tests, nor do they indicate a complete loss of fertility after 8 min (Rutter), 3 min (Smirnov), or a low percentage at 30 sec (Shuman). Ova were fertilized by spermatozoa held in water for as long as 8 hr (10.9%) and in the same year (1931) a sample of milt held for 90 min fertilized 91.5% of the sample of ova added to it.

As shown in Table I there was great variability in the percentage fertilization of ova treated with the milt samples. In many samples there was no fertilization; in 1933, none of the samples, held for periods of from ½ to 12 hr, fertilized freshly-added eggs. The reason for the variable fertilizability may be ascribed to the quality of the males stripped. The differences in percentage fertilization where duplicate samples were used — 1927 and 1928 — confirm this, since different males were used for each sample. The complete failure to get any fertilization whatever in 1933 in the samples retained for from 1 to 12 hr is puzzling.

The results (Table I) indicated that:

(a) After 30 min retention of well-diluted milt in water, 60.1% and 26.8% of the ova taken in 1927 were fertilized, whereas no fertilization occurred in 1928 and 1929, 2% in 1931, and none in 1933;

(b) After 60 min retention, 72.1% and 0.4% of the ova taken in 1928 were fertilized, only 0.4% and 0.5% in 1929 and 1931, respectively, and none in 1933;

(c) After 90 min retention, 5.0% and 91.5% of the ova taken in 1929 and 1931, respectively, were fertilized, but none in 1933;

(d) After 7½ hr retention of well-diluted milt in water, 22.8% of the ova tested in 1931 were fertile, and after 8 hr retention, 10.9%.

TABLE I. Percentage fertilization of sockeye salmon eggs when spermatozoa were used which had been retained in water for varying periods of time before fertilization.

Minutes	1926			1927			1928			1929			1931			1933[a] and 1934		
	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed
2	350	32	9.1													238	119	50.0
4	353	73	21.0													409	97	23.7
5										201	1	0.5						
6	274	22	8.0													531	86	16.2
8	240	53	13.8													462	1	0.2
10	586	83	14.2				342	0	0.0									
12	262	20	8.0				374	0	0.0	93	0	0.0				363 252	4 0	1.1 0.0
14	215	38	17.7													218	0	0.0
15							336	0	0.0									
							436	0	0.0	360	50	14.0				230	0	0.0
16	272	210	77.2	1128	774	68.6												
				1056	65	6.1												
18	350	41	11.7	924	135	14.6												
				981	129	13.1												
20	212	11	5.2	600	39	6.5	550	0	0.0									
				1267	678	53.5	623	0	0.0	325	51	15.7						
22				735	220	30.0												
				1008	90	0.9												
23				732	257	35.1												
				1147	389	33.9												
24				812	32	4.0												
				1212	470	38.7												
25				914	296	32.4	650	0	0.0									
				1237	251	20.3	717	0	0.0	202	36	17.8						
26				945	37	4.0												
				1451	548	37.8												

27		1522	424	27.8								
		1347	501	37.2								
28		1340	407	30.4								
		1911	858	43.3								
29		2426	121	25.6								
		1907	436	22.8								
30		1648	993	60.1	425	0	0.0					
		1962	527	26.8	443	0	0.0	311	0	0.0	758	15	2.0
35					739	15	2.0					
					765	18	2.4	327	1	0.3		
40					1309	1	0.1					
					1027	1	0.1	414	0	0.0		
45					969	0	0.0					
					675	66	9.8	691	11	1.6		
50					614	200	32.6					
					714	242	33.9					
55					44	4	9.0					
					44	14	31.8	255	60	23.5		
60					584	421	72.1					
					694	3	0.4	251	1	0.4	644	3	0.5
65					938	315	33.6					
					643	80	12.4					
70					571	55	9.6					
					718	16	2.2					
75					672	7	1.0					
					440	142	32.3	388	49	12.6		
80					602	0	0.0					
					627	5	0.8	236	8	3.4		
85												
90								443	22	5.0	306	280	91.5
105								243	5	2.1		
120											327	5	1.5
140					613	87	14.2					
150											709	62	8.7
180											700	12	1.7

(Continued)

TABLE I. Percentage fertilization of sockeye salmon eggs when spermatozoa were used which had been retained in water for varying periods of time before fertilization. — (*Concluded*)

Minutes	1926			1927			1928			1929			1931			1933[a] and 1934		
	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed
210													919	0	0.0			
240													483	7	1.4			
270													492	1	0.2			
300													523	0	0.0			
330													492	0	0.0			
360													563	5	0.9			
390													258	3	1.2			
420													571	130	22.8			
450													777	24	3.1			
480													587	64	10.9			

[a]Samples of milt were held in 1933 up to 12 hr, at 1-hr intervals. There was no survival in any of the samples.

It is thus suggested that spermatozoa may be capable of fertilizing eggs for a remarkably long period of retention in water after release from the mature male. In the present experiments the sperm suspensions were well diluted and thoroughly shaken. Therefore, though the milt subsequently settled gradually to the bottom of the jars and had to be thoroughly mixed again prior to use, there could be no likelihood of conditions developing wherein isolated drops of concentrated sperm suspension retained, by reason of their crowded condition and consequent inactivity, their vitality until finally agitated by pouring out the liquid, as might be inferred from the conclusions of Gray (1928) for spermatozoa of *Echinus*.

For sockeye salmon ova, the data (Table II) indicate that the fertilizable period, after extrusion into water, may extend to 28 min but with a diminishing degree of fertility. The inverse relationship between percentage fertilization and period of retention in water reported by Rutter (1902) was clearly evident in two of the years (1926 and 1931) but less markedly so in the other years. Experiments by Smirnov (1963) with pink salmon gave similar results. He records for one of two series of tests, that "the capacity to be fertilized gets less & less with the time of retention in water and after 9 minutes is practically gone."

The results thus suggest that under natural conditions the ova, rather than the spermatozoa, may constitute the limiting factor, as it were, in delayed insemination. Though it is unquestionably desirable that mixing of the sex products take place as soon after extrusion as possible, it cannot be inferred that a delay in fertilization, by reason of temporary absence of the males at time of egg deposition, is indicative of nonfertilization *unless* the eggs are immediately covered up with gravel by the female. Furthermore, the fate of ova expressed by females spawning unattended by males by reason of a deficiency in the numbers of the latter may not be as critical as previously supposed. With spawning males functioning throughout a spawning area the dispersion and settling of sperm suspensions over and percolating through the gravel may well lead to contact with the ova deposited by unattended females and result in the fertilization of a part, at least, of the eggs. The experiments of Shuman (1950) negate this suggestion, however.

It is of interest to compare the foregoing results with the losses which were found to occur under ordinary circumstances, in the Cultus Lake hatchery, from the time the eggs were placed in the troughs up to the time they had reached the "eyed" stage, for 6 years when accurate detailed records were kept. These were as follows: 4.5, 8.2, 6.2, 10.5, 6.4, 11.6%, or an average of 7.9% of the total eggs placed in the hatchery baskets for incubation. In other words, an average of 92% of the eggs reached the eyed stage successfully.

RETENTION IN AIR. The results (Tables III and IV) indicate that retention in air, i.e. with no water added, has no deleterious effect on fertility for quite some time after expression from the fish. Until what appears to be chemical decomposition occurs, a high percentage of fertilization is obtained. Over 90% fertilization occurred of ova, treated with milt that had been retained

TABLE II. Percentage fertilization of sockeye salmon eggs retained in water for varying periods of time before fertilization.

Minutes	1926			1927			1929			1931			1933			1934		
	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed
													349	26	7.5			
2	472	221	46.8							245	53	21.6	305	6	2.0	321	20	6.2
							298	15	5.0									
3							234	2	0.9				345	19	5.5			
4	458	119	26.0							325	40	12.3	338	14	4.1	216	10	4.6
							226	0	0.0									
5							182	1	0.6				327	5	1.5			
6	634	122	19.2							365	32	9.0	378	5	1.3	173	1	0.6
							271	0	0.0									
7							271	3	1.1				311	1	0.3			
8	494	35	7.1							408	30	7.3	377	2	0.5	190	2	1.1
							276	0	0.0									
9							285	1	0.3				304	1	0.3			
10	411	18	4.4							504	15	3.0	?	0	0.0	197	1	0.5
							285	1	0.4									
11													—	0	0.0			
12	628	23	3.6	192	0	0.0				362	4	1.1	375	2	0.6	228	0	0.0
							159	0	0.0									
13							339	1	0.3									
14	613	3	0.5	244	0	0.0							?	0	0.0	153	0	0.0
							330	0	0.0									
15							387	1	0.2				?	0	0.0			
16	653	15	2.3	343	1	0.3							?	0	0.0			
18	719	43	6.0	304	0	0.0	(Remainder of samples up to 40 min showed total loss.)						?	0	0.0			
20	655	2	0.3	283	1	0.3							?	0	0.0			
22													?	0	0.0			
24													?	0	0.0			
													257	7	2.7			
26													232	8	3.4			
28													?	0	0.0			
30																		

up to 25 hr in the 1928 test. Longer periods of retention in later years resulted in much lower percentages of fertilization. For ova, retention in a relatively dry state up to 96 hr resulted in approximately 80% fertilization in the 1931 tests. In other years the results were much more variable and appreciably lower, on the average dependent no doubt, as earlier intimated, on the condition of the males available for stripping.

Rutter (1902) recorded for chinook salmon ova held in air, at a temperature of 76 C, a percentage fertilization of 100 at 12 min, 99 for 30 min, and 76 for 50 min. Kawajiri (1927), for *O. masou*, stated that "the egg and sperm maintain the fertilizing power after having been kept during 24 hours within 1.0°–14.9°C." The latter author further correlated the preservation of fertility during retention in air after 48 hr with temperature: 48 hr at 16 C, 72 hr at 12 C, and 96 hr at 9.3 C. He ascribed the decline in fertilizing power of both sperms and ova to chemical change.

In tests to determine the practical possibilities of holding fresh, ripe milt of steelhead (*Salmo gairdneri*) and chinook salmon (*O. tshawytscha*) for shipment to spawning areas where male fish are scarce for artificial stripping. Smith and Quistorff (1943) found that:

(a) For steelhead, holding periods of 2.5 and 5 hr produced hatching losses of 96.8% and 99.7%, respectively, in contrast to a 4.2% loss in controls with normal fertilization;
(b) For chinook salmon, however, similar holding periods of 2.5 and 5 hr gave hatching mortalities of 9.5% and 45.9%, respectively, while in a control sample with no retention the loss was 6.1%;
(c) When milt from male chinook salmon, killed but not stripped for 2.5 and 5 hr after death, was used hatching mortalities of only 5.5% and 7.1%, respectively, occurred.

From somewhat similar retention tests with chum salmon (*O. keta*) at air temperatures of 2.5–5.8 C, Barrett (1951) obtained the following results:

(a) For chum salmon ova, held in dry sterile jars for 72 hr prior to adding milt, less than 10% were infertile, after 108 hr 20% were infertile, and after 108 hr the percentage of infertile eggs rose to a maximum of 85% after 8 days;
(b) For chum salmon spermatozoa a wide range of mortalities occurred as a result of storage prior to application to ova. For retention up to 36 hr, 10 of 12 samples had less than 5% infertility. From 0 to 96 hr storage, 24 of 32 samples had less than 50% infertility, mean 8.9%. From 96 to 192 hr holding, 24 of 32 samples showed greater than 50% infertility.

It may be noted that in Barrett's experiments, fertilization of the eggs was determined by microscopic examination of the germinal disc after 24 hr incubation. In the fertilized egg the first to fourth cleavages were plainly visible on the germinal disc.

From the results here reported and those already in the literature it is apparent that for artificial propagation of Pacific salmon the periods of time during which ova and spermatozoa may be held prior to fertilization, namely,

TABLE III. Percentage fertilization of sockeye salmon eggs when spermatozoa were used which had been retained in air (i.e. without addition of water) for varying periods of time before fertilization.

Hours	1926			1927			1928			1929			1931			1933		
	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed
	249	246	99.0															
0.5	391	43	11.0															
	317	293	92.5															
1.0	941	656	69.7															
	196	124	63.3										(Samples of milt held for periods of 48-96 hr, at hourly intervals. There were no survivals in any of the samples)					
1.5	708	417	58.9															
	236	184	78.0															
2.0	617	414	67.1															
	421	376	89.3															
2.5	689	598	86.8															
	573	425	74.2															
3.0	834	707	84.8															
	686	548	79.9															
3.5	591	496	83.9															
	691	584	84.5															
4.0	593	541	91.2															
	939	749	79.8															
4.5	849	513	59.3															
	907	530	58.5															
5.0	960	247	25.8															
	844	766	90.8															
5.5	626	441	70.5	1512	541	35.8												
	677	490	72.4															
6.0	1013	704	69.5	1106	454	41.0												
	807	758	93.9															
6.5	599	392	65.5	1499	0	0.0												
	916	888	96.9															
7.0	758	149	19.7	1183	920	77.7												
	733	25	3.3															
7.5	836	764	91.4	1600	948	59.3												
	501	70	14.0															
8.0	1173	1094	93.3	1515	611	40.3												
8.5				1438	1095	76.1												
9.0				764	691	90.5												

9.0			764	691	90.5						
9.5			805	672	83.5						
10.0			1371	960	70.0	797	793	99.5			
10.5			1414	1090	77.1	471	471	100.0			
11.0			1197	762	63.7	548	539	98.3			
11.5			1054	441	41.8	453	448	98.9			
12.0			1265	787	62.2	705	692	98.1			
13.0						623	612	98.2			
14.0						670	553	82.5			
15.0						768	747	97.3			
16.0						968	862	89.0			
17.0						1103	1068	96.8			
18.0						1091	1063	97.4			
19.0						1158	1137	98.2			
20.0						1099	962	87.5			
21.0						947	821	86.6			
22.0						903	835	92.5			
23.0						937	914	97.5			
24.0						685	676	98.7			
25.0						434	426	98.1			
26.0						789	729	92.4			
27.0						514	297	57.7			
						845	801	94.8			
						517	497	96.1			
						666	645	96.8			
						804	697	86.7			
						753	659	87.5			
						826	769	93.1			
						596	592	99.3			
						663	655	98.3			
						763	738	96.7			
						868	844	97.2	725	11	1.5
						734	717	97.7			
						513	493	96.1	912	33	3.6
									435	0	0.0
									—	—	—

TABLE III. Percentage fertilization of sockeye salmon eggs when spermatozoa were used which had been retained in air (i.e. without addition of water) for varying periods of time before fertilization. — (*Concluded*)

Hours	1926			1927			1928			1929			1931			1933		
	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed
28.0										925	45	4.9				388	17	4.4
29.0										819	10	1.2						
30.0										—	0	0.0						
31.0										—	0	0.0						
32.0										—	0	0.0				485	3	0.6
33.0										—	0	0.0						
34.0										—	0	0.0						
35.0										—	0	0.0						
36.0										1004	411	40.9				?	0	0.0
37.0										896	226	25.2						
38.0										1332	394	3.0						
39.0										921	177	19.2						
40.0										785	177	22.5				?	0	0.0
41.0										815	172	21.1						
42										618	26	4.2						
43										501	60	11.9						
44										512	17	3.3				?	0	0.0
45										449	31	7.0						
46										380	174	46.0						

45								
46					380	174	46.0	
47					834	28	3.3	
48					1185	24	2.0	
52								455 0 0.0
56								457 9 1.9
60								362 50 13.8
64								? 0 0.0
68								? 0 0.0
72								? 0 0.0
								409 18 4.4 (samples held up to 96 hr, no survivals)

TABLE IV. Percentage fertilization of sockeye salmon eggs, retained in air (i.e. without addition of water) for varying periods of time before fertilization.

Hours	1926			1927			1928			1929			1931			1933		
	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed	Total eggs	Total eyed	Per-centage eyed
	496	303	61.0															
0.5	386	315	81.6															
	395	365	93.4															
1.0	405	333	82.2															
	478	292	61.5															
1.5	385	245	63.7															
	465	431	92.7															
2.0	404	281	69.6															
	648	396	61.1															
2.5	417	332	79.7															
	430	234	54.4															
3.0	531	245	46.2															
	329	297	74.0															
3.5	568	471	82.9															
	804	645	80.2															
4.0	449	342	76.2															
	519	412	79.5															
4.5	486	404	83.2															
	845	756	89.5															
5.0	493	388	78.7															
	669	508	75.9															
5.5	471	374	79.4															
	432	329	75.0															
6.0	420	265	63.0															
	363	241	66.4															
6.5	658	524	79.7	1187	1046	88.1												
	503	268	53.3															
7.0	568	462	81.4	1247	1051	84.3												
	929	696	74.9															
7.5	455	310	68.1	921	600	65.1												
	300	193	64.2															
8.0	650	592	89.5	814	659	84.6												
8.5				1145	588	51.4												

8.5			1145	588	51.4						
9.0			1192	607	50.9						
9.5			1047	601	57.4						
						321	238	74.1			
10.0			913	280	30.6	255	214	84.0			
10.5			1095	606	55.3						
						420	341	81.2			
11.0			1098	444	40.4	345	265	76.8			
11.5			1074	487	45.3						
						416	285	68.5			
12.0			1327	952	71.7	434	360	83.0			
						471	123	26.1			
13.0						420	316	75.2			
						384	291	75.8			
14.0						315	218	69.2			
						452	336	74.3			
15.0						352	204	58.1			
						359	238	66.3			
16.0						347	215	62.0			
						295	194	66.0			
17.0						414	238	57.5			
						511	343	67.1			
18.0						551	273	49.5			
						391	279	71.4			
19.0						503	376	74.7			
						685	465	67.9			
20.0						553	257	46.5			
						469	243	51.8			
21.0						389	191	49.1			
						582	271	46.5			
22.0						635	87	13.7			
						670	381	57.0			
23.0						539	245	45.4			
						564	9	1.6			
24.0						497	17	4.0	616	403	65.4
						259	97	37.4			
25.0						292	212	72.6	689	452	65.6
26.0									904	680	75.2
27.0									935	672	71.9

(*Continued*)

TABLE IV. Percentage fertilization of sockeye salmon eggs, retained in air (i.e. without addition of water) for varying periods of time before fertilization. (*Continued*)

Hours	1926			1927			1928			1929			1931			1933		
	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed
28.0										639	307	48.0						
29.0										610	397	65.1						
30.0										520	318	61.1						
31.0										556	383	68.9						
32.0										413	288	69.7						
33.0										571	346	66.0						
34.0										836	563	67.3						
35.0										1544	940	60.9						
36.0										456	282	61.8						
37.0										589	354	60.1						
38.0										476	164	34.4						
39.0										530	292	55.1						
40.0										568	392	69.0						
41.0										706	388	55.0						
42.0										525	262	50.0						
43.0										618	276	44.7						
44.0										397	214	53.9						
45.0										557	313	56.2						

46.0				943	633	67.1		
47.0				864	608	70.4		
48.0				1309	875	66.8		
50.0								
52.0								
54.0								
56.0								
58.0								
60.0								
62.0								
64.0								
66.0								
68.0								
70.0								
72.0								
74.0								
76.0								
78.0								
80.0								
82.0								
84.0								
86.0								

576	516	89.6			
584	510	87.3			
389	319	82.0			
367	271	73.8			
347	298	86.0			
377	317	83.1			
345	296	85.8			
436	386	88.5			
302	244	80.8			
440	384	87.3			
301	253	84.0			
380	318	83.0			
394	357	90.6	339	288	85.0
637	550	81.7			
496	386	77.8	365	224	61.4
499	444	88.9			
531	463	87.2	453	8	1.8
526	435	82.7			
363	315	86.8	—	—	—
531	459	864.			

(Continued)

TABLE IV. Percentage fertilization of sockeye salmon eggs, retained in air (i.e. without addition of water) for varying periods of time before fertilization. — (*Concluded*)

Hours	1926			1927			1928			1929			1931			1933		
	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed	Total eggs	Total eyed	Percentage eyed
88.0													492	411	83.5	495	291	60.0
90.0													646	562	87.0			
92.0													681	585	86.0			
94.0													559	451	81.6			
96.0													453	334	73.7	304	0	0.0
104.0																521	1	0.2
112.0																441	1	0.2
120.0																296	1	0.3
136.0																405	1	0.25
																(Sample held up to 192 hr but no survival beyond 136 hr.)		

24–36 hr for spermatozoa and 96–108 hr for ova, are quite extensive and probably well within the limits of practical usefulness. Further studies may well extend the periods with the use of special techniques, particularly refrigeration.

SUMMARY

Experiments were undertaken at Cultus Lake, British Columbia, over the years 1926–34 to determine the effect on fertility of sockeye salmon spermatozoa and ova of periods of retention (a) in water, and (b) in air prior to application of the opposite sex product. The tests were carried on over a number of seasons, the periods of retention being extended in successive years in order to reach the upper limit of time. In some cases experiments were repeated in order to duplicate previous tests.

Samples of spermatozoa held in water for 8 hr were found to fertilize 10.9% of a sample of ova to which they were added; a fertilization of 91.5% was obtained after 1½ hr retention. Great variability occurred, presumably due to the variable condition of the male fish used. This was apparent from the differences in percentage fertilization obtained with duplicate tests in some of the years.

Ova held in water for varying periods maintained fertility up to 28 min. From 2 min (46.8% ova fertile) to 12 min (3.6% ova fertile) the decrease in fertility was rapid.

The deleterious effect of retention in air, i.e. before adding water, became noticeable after 25 hr for spermatozoa and after 96 hr for ova.

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Estimation of Sea Mortality Rates for the 1961 Brood-Year Pink Salmon of the Bella Coola Area, British Columbia[1]

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ABSTRACT

A two-stage marking experiment was designed to estimate natural mortality rates of pink salmon during their early (coastal) and later (oceanic) periods of sea life. Difficulty was encountered because of disproportionate representation of various stocks in the marked populations, the stocks being subject to dissimilar rates of exploitation. Several assumptions were made for which the error introduced could not be fully evaluated. Under these assumptions, the results indicate (approximate values) that 55.7 million fry, resulting from the 1961 Burke Channel–Bella Coola stocks brood year, entered the sea. Of these, 77% died during the initial 40-day period of life in the enclosed marine waters. The following stage, from the time of seaward migration to adult return, a period of about 410 days, 78% of the remaining population died. The adult return was subjected to a rate of exploitation of 0.85 which produced a catch of 2.5 million fish. The spawning escapement was approximately 450,000 fish. It is established that the rate of natural mortality during the initial short period was much more severe than that during the remaining period of sea life.

INTRODUCTION

In previous studies it has been inferred that the natural mortality rate in the sea is higher for the younger, smaller salmon. Ricker (1962), considering data of sockeye salmon (*Oncorhynchus nerka*), demonstrated that larger smolts entering the sea survived better than smaller smolts in both inter- and intra-stock comparisons. Parker (1962a), as a result of comparisons between the measured survival rates and average fecundities of pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) proposed a relatively high initial instantaneous mortality rate, termed "coastal" followed by a relatively low "oceanic" rate. Using sockeye data, a model depicting these two successive mortality stages was developed and explored (Parker, 1962b). This model appeared to give adequate explanation for the available facts. Fredin (1963) has proposed several possible schemes for distribution of ocean mortality rates and explored their consequences on one stock of sockeye. In a more recent study Fredin (1965) has extended his methods and applied them to two large North American stocks. While these studies serve a useful function in developing theory and as approaches for understanding sea mortality, it remains to be demonstrated clearly that early sea mortality rates actually differ from those applicable to the later period of sea life.

A previous study (Parker, 1964) of pink salmon, utilizing marking by fin removal, failed to provide a valid estimate of the natural mortality rate

[1]Received for publication May 19, 1965.

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

prevailing during a specified time period after entrance of fry into the sea. The failure was due primarily to the involvement of two different stocks of fish. For the first marking, seaward-migrating fry were marked and liberated in Hook Nose Creek (Fig. 1). The second marking, although conducted off the estuary of Hook Nose Creek, involved fingerlings captured in the sea where the Hook Nose Creek stock formed only a minor fraction of the population. Later events were interpreted as indicating that most of the juvenile population associated with the second marking was native to Dean Channel streams. Although a single fishery was involved in catching adults of these two stocks it was discovered that they were subject to totally dissimilar rates of exploitation. The Hook Nose Creek stock entered the fishing area and remained vulnerable for some time while, in contrast, the Dean Channel stock moved rapidly through the fishery and into an area where commercial fishing was prohibited. It was possible to estimate quite accurately the rate of exploitation of the

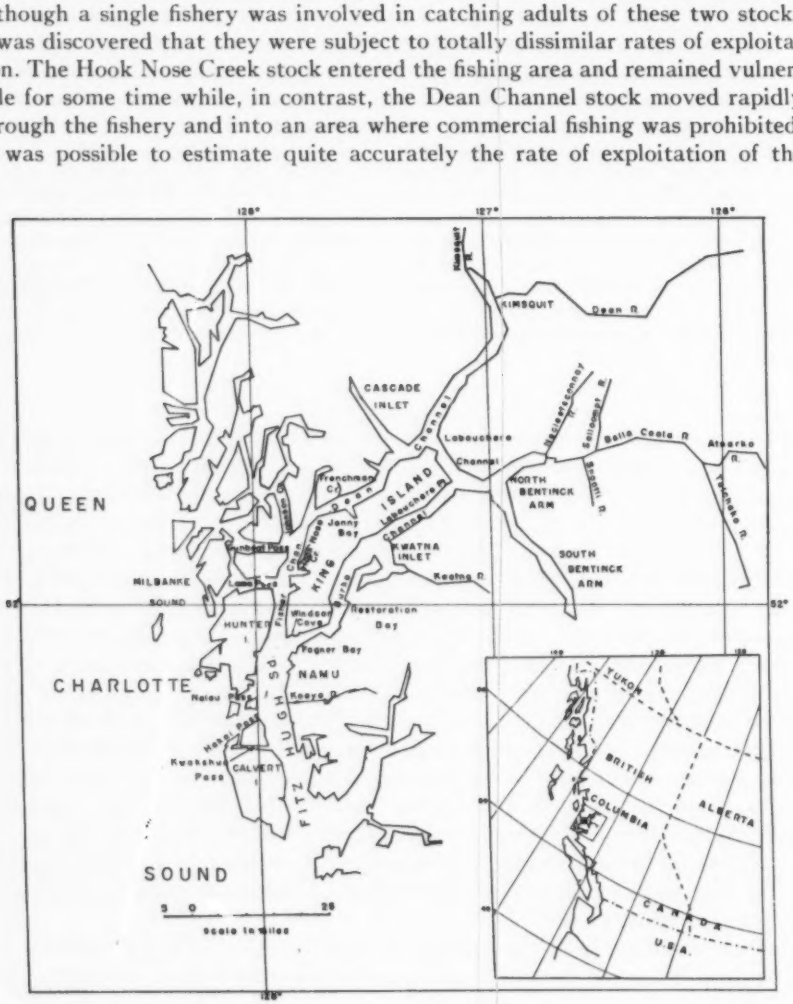

FIG. 1. The central area of the British Columbia coast.

Hook Nose Creek stock for the spawning population was accurately enumerated. However, it was not possible to estimate the rate of exploitation of the Dean Channel stock, except to indicate that it was much lower. As a consequence, the returns of the two marked populations could not be weighted to provide an estimate of early sea mortality rate.

In general, the most important pink salmon run of the central British Columbia coast is that to the Bella Coola River system. In 1962, the run to this system was the largest on record, providing an estimated commercial catch of about 12 million fish (Parker, 1964). Based on the seasonal pattern of the fishery in 1962, Bella Coola adult pink salmon appeared to enter Fitz Hugh Sound primarily from the south and west, and to a lesser degree from Milbanke Sound through Fisher Channel. These fish then moved into Burke Channel, of which the portion lying southwest of Kwatna Inlet was closed to commercial fishing. In Burke Channel above this sanctuary and in North Bentinck Arm a gillnet fishery removed a significant portion of the remaining population before it entered the Bella Coola River. Neither of the marked populations were significantly involved in the Upper Burke Channel–North Bentinck Arm catches. Similar to the stocks represented by the second mark, the Bella Coola stocks appeared to pass right through and not remain available to the Fisher Channel–Fitz Hugh Sound fishery as did the Hook Nose Creek and, presumably, other local stocks.

The progressive dilution of Hook Nose Creek marked pink salmon fry and fingerling by other similar-sized stocks in Fisher Channel and their complete submergence in the Bella Coola stock in southern Fisher Channel and Fitz Hugh Sound was apparent from the examination of fingerling catches in 1961. This observation suggested that a two-stage marking experiment might yield a reliable estimate of early sea mortality but only if both markings involved predominately a single stock. That of the Bella Coola River appeared to offer the best opportunity. A second two-stage marking experiment was therefore attempted on the 1961 brood-year Bella Coola stock and the interpretation of the results forms the subject of this report.

THE JUVENILE POPULATION

In 1961 large accumulations of pink salmon fingerlings were observed at the confluence of Burke Channel and Fitz Hugh Sound during late April and May. These, from their great numbers, were thought to be components of the dominant Bella Coola stock. It was further observed that a large portion of the populations present in Fisher Channel, Burke Channel, and northern Fitz Hugh Sound passed through Nalau Pass on their migration from these enclosed waters into Queen Charlotte Sound. This migration occurred during late May and early June. It was somewhat naively assumed that fish captured and marked in early May 1962, at the mouth of Burke Channel would, in all likelihood, be very preponderantly Bella Coola stock. It was further assumed that the same preponderance would apply to a second marking made as fish migrated through Nalau Pass in early June.

Accordingly, a marking site was established in Fogner Bay on the mainland side of Burke Channel near Fitz Hugh Sound. Fingerling pink salmon were captured with a small seine at the confluence of Burke and Fisher Channels, transported across Burke Channel to the marking site and held overnight or longer in floating ponds before marking. Under anaesthesia, fish were marked by removal of the adipose and right ventral (ARV) fins and subsequently held until late in the following day before release. Prior to each release a sample (N = 600) was examined under magnification to ascertain the quality of marking. From these data the daily releases of various marks were calculated. Totals for the season are presented in Table I. Fish were released during the period May 5–14 and only a small fraction, less than 1.5% of the total, were mismarked.

TABLE I. Releases of marked pink salmon, 1962, Fitz Hugh Sound area, British Columbia.

Mark	Burke Channel May 5–14	Nalau Pass June 2–6
ARV	181,966	0
RV	864	0
A	950	0
ABV	898	227
BV	0	0
ALV	0	112,858
LV	0	719

The marking station was then moved to Nalau Pass and a second lot of fish was similarly obtained and processed. These, marked by removal of the adipose and left ventral (ALV) fins, were released during the period June 2–6. The estimated total releases of various marks are presented in Table I. Less than 0.8% of these fish were mismarked. The mismark adipose both ventral (ABV) combination is common to both markings and fish bearing such marks were therefore eliminated from further consideration.

During the earlier marking period many fish were found with naturally missing or mutilated fins. This damage was found to result from chalimus larvae of a parasitic copepod *Caligus clemensi* (see Parker and Margolis, 1964). In some samples more than 10% of the fish were infected with this parasite, resulting in damage of varying degrees. These larvae attach by a frontal filament to a bony structure of the fish and feed on those tissues which can be reached in an arc from the point of attachment. A bony part appears necessary for attachment of this parasite and all rayed fins were liable to attack and mutilation as well as the operculi and branchiostegals. No case of copepod

mutilation of the adipose fin was observed in the several thousands of infected fish examined. During the second marking, chalimus larvae were also present, to a lesser degree, on juvenile salmon. At this time, however, the hosts were much larger in relation to the size of the parasite, and fin damage was negligible.

It is concluded that fish with mutilated or missing ventrals can only be distinguished later as either deliberately or accidentally (copepod) marked fish by the presence or absence of the adipose fin. Therefore the single fin releases (RV and LV) shown in Table I must also be eliminated from consideration in the experimental results. There is also the chance that some fraction of fish marked ARV would lose the LV fin to the copepods, thus becoming ABV. Furthermore, some fraction of the calculated 950 adipose-only releases from the first marking may have become ARV, ALV, or ABV from chalimus infection. However, such occurrences would be relatively rare and the effect of such changes of identity on the calculations would be negligible.

The origin of stocks comprising the two marked populations is uncertain. There are two lines of evidence which may be examined to throw light on this question: (1) direct observations of abundance of fingerlings at various localities and (2) the comparison of sizes of fish marked at the two locations.

Although observations on the distribution of pink salmon fry and fingerlings began in mid April, few were seen in Burke Channel until the later part of that month. At the west end of Burke Channel, a small school was observed on April 23 in Windsor Cove. On April 25 a small school (estimated at 5000) was sighted on the south shore of Burke Channel just east of Fogner Bay. No fish were seen further eastward in Burke Channel as far as Kwatna Inlet, where a school of many thousands, obviously recently emerged fry, was found north of Kwatna River. Juvenile salmon were present in fair abundance in the vicinity of Labouchere Point on April 26 but none was seen between that location and Kwatna Inlet. On April 27 the waters of North Bentinck Arm were searched and salmon fry were very abundant along all shores. Schools of fry were also seen in mid channel in the eastern sector of North Bentinck Arm, off the mouth of the Bella Coola River. Very few fish were seen in Labouchere Channel beyond its confluence with Burke Channel. While these observations are far from exact they are presented more or less quantitatively in Fig. 2 for the time period April 23–27. The area searched is enclosed within the dashed line of this and subsequent figures.

During the period May 1–3, observations were continued in Fisher and Dean Channels and again in Burke Channel. Fish were generally scarce or absent in Fisher and Dean Channels. Small numbers were sighted close to known salmon-producing streams but were not in any case abundant. On the other hand, schools were large and abundant around and west of Labouchere Point. In this vicinity fish were evidently accumulating, presumably from North Bentinck Arm; however, the distribution did not extend as far as Kwatna Inlet. These observations are presented in Fig. 3.

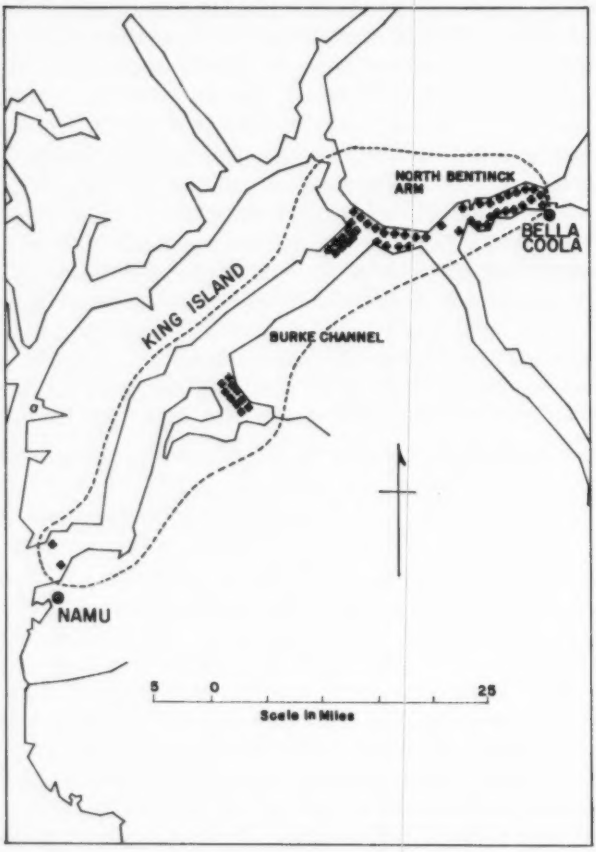

FIG. 2. Distribution of juvenile pink salmon schools, April 23–27, 1962. Dashed line encloses area searched.

On May 7, fish were accumulating along the King Island shore at the confluence of Burke and Fisher Channels. Across Fitz Hugh Sound, a few schools of fish were sighted along the eastern shore of Hunter Island north of Nalau Pass. Fish were not observed in Nalau Pass or in Hakai Pass. These observations are presented in Fig. 4.

During the period May 11–13 a very large accumulation of pink salmon fingerlings was observed at the confluence of Kwatna Inlet and Burke Channel. Salmon appeared to be nearly absent in North Bentinck Arm, but were present in Burke Channel as far as Kwatna. The schools, while found in protected areas, were generally off the beach at this time. These observations are presented in Fig. 4.

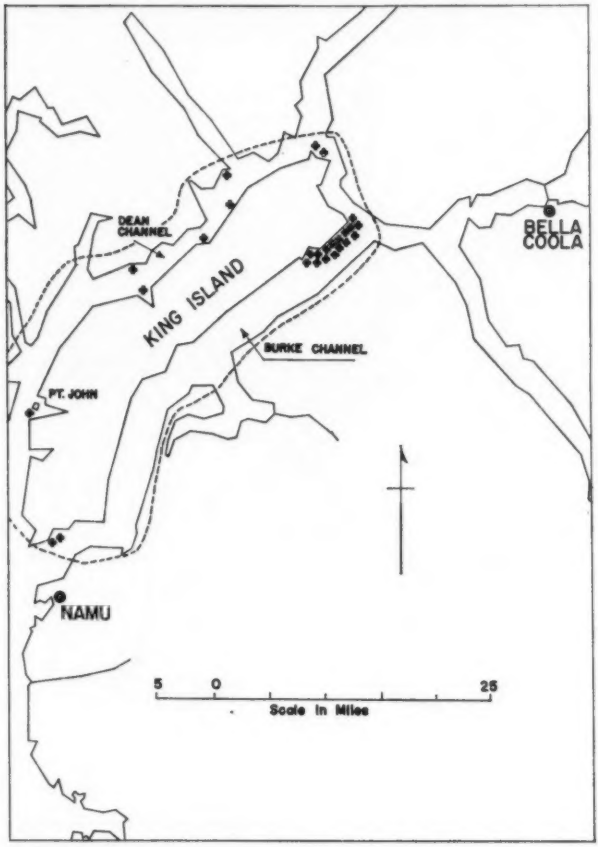

FIG. 3. Distribution of juvenile pink salmon schools, May 1–3, 1962. Dashed line encloses area searched.

On May 17, schools of salmon were abundant at the Fitz Hugh Sound approaches to Nalau Pass. A small accumulation (less than 10,000) was found in Fitz Hugh Sound at Kwakshua. Along Calvert Island, and along the mainland shore north to Namu, fish were present in small and insignificant numbers. At the confluence of Burke Channel with Fitz Hugh Sound and Fisher Channel, the accumulations had obviously increased since the last observations. Schools were sighted throughout the length of Burke Channel as far as Labouchere Point. The main center of abundance was again at the entrance to Kwatna Inlet.

On May 19 and 20, fish were not found in any significant quantity in Labouchere, Dean, or Fisher Channels, nor were they found in Johnson Channel, Gunboat Pass, or Lama Pass. From a point on Hunter Island opposite the

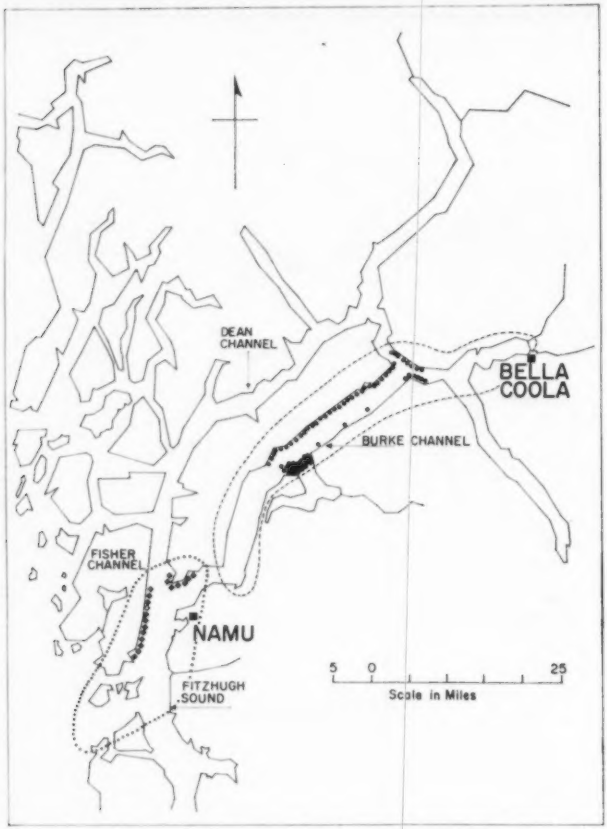

FIG. 4. Distributions of juvenile pink salmon schools, May 7 (+) and May 11–13 (•), 1962. Areas searched are enclosed by dashed and dotted lines.

north entrance to Burke Channel, fish became increasingly abundant toward Nalau Pass. Again, few fish were observed in Nalau Pass. These observations are presented in Fig. 5.

During the period May 21–29, fish continued to accumulate in lower Burke Channel and along the Hunter Island shore north of Nalau Pass. On May 30, pink salmon began to enter Nalau Pass and temporarily accumulated there, reaching an apparent peak of abundance on June 5 and 6. Fish were not observed in Fisher Channel above Burke Channel. Accumulations in Burke Channel diminished and disappeared. Many schools were sighted in mid channel in northern Fitz Hugh Sound and western Burke Channel. On June 10, the accumulations in Nalau Pass were noticeably smaller and fish were scarce there on June 12. During the period June 8–12 several schools of juvenile

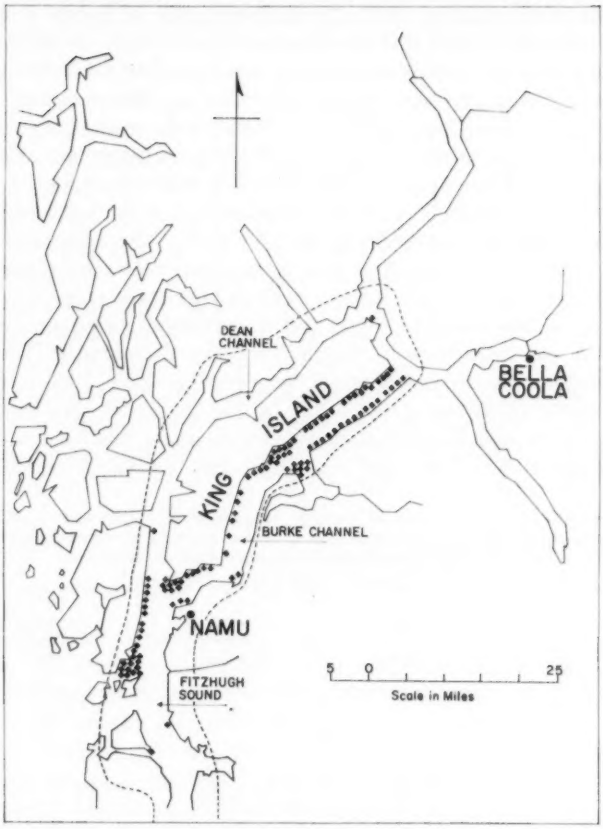

FIG. 5. Distribution of juvenile pink salmon schools, May 17–20, 1962.

pinks were found off the seaward approaches to Nalau Pass in Queen Charlotte Sound.

These observations suggest that pink salmon were generally absent or of insignificant numbers within the study area except along a direct route from the Bella Coola River through Nalau Pass to the open waters of Queen Charlotte Sound. Unfortunately, the early marking took place at a time when the main concentrations of Bella Coola stocks still were in upper Burke Channel and had not yet reached the marking site in strength. During the time of fishing for this marking only small numbers of fish were available. Often the scarcity of fish controlled the numbers marked. It is quite possible that this early marking involved large proportions of small local stocks, as well as smaller portions of Kwatna and Bella Coola stocks which had, either by passive displacement by the strong Burke Channel tidal currents, or by active and

directed swimming, arrived early at the confluence of Burke Channel with Fisher Channel–Fitz Hugh Sound. The second marking, on the other hand, took place when large concentrations were no longer present in Burke Channel and heavy accumulations were present in Nalau Pass. It is presumed, therefore, that the second marking involved mainly Bella Coola stocks of pink salmon.

The second line of evidence regarding the origin of the marked populations is through a comparison of sizes of fish marked at both locations. Three samples of pink salmon, preserved in seawater formalin, are available to represent the length frequency of the first marking, the ARV group. These were obtained from the catches taken for this marking. One sample was preserved to represent the size frequency of fish from the second marking, the ALV group. Both samples were measured to the nearest 0.1 cm, and the results of grouping these data by 0.1 unit of natural logarithms of length (Ln l) are presented in Table II. The instantaneous growth rate in length (g), on a per-day basis, is given by LeBrasseur and Parker (1964) as $g = 0.0186$. In Fig. 6, equal area curves of the grouped length frequencies are presented 25 days apart, the time lapse between the 50% release dates of the two markings. Two dashed lines are drawn in,

TABLE II. Comparison by length frequency of ARV and ALV marked populations of pink salmon at time of marking (grouped by 0.1 Ln l intervals), Fitz Hugh Sound area, British Columbia.

Group (l in cm)	Ln l (midpoint)	First ARV marking	Second ALV marking
		%	%
3.1–3.3	1.15	0.8	...
3.4–3.6	1.25	10.9	...
3.7–4.0	1.35	18.4	...
4.1–4.4	1.45	15.5	...
4.5–4.9	1.55	19.1	0.2
5.0–5.4	1.65	15.8	3.0
5.5–6.0	1.75	13.7	9.4
6.1–6.6	1.85	4.8	28.4
6.7–7.3	1.95	1.0	43.2
7.4–8.1	2.05	...	14.0
8.2–9.0	2.15	...	1.8
Total:		100.0	100.0
No. of samples:		3	1
No. of fish:		770	504

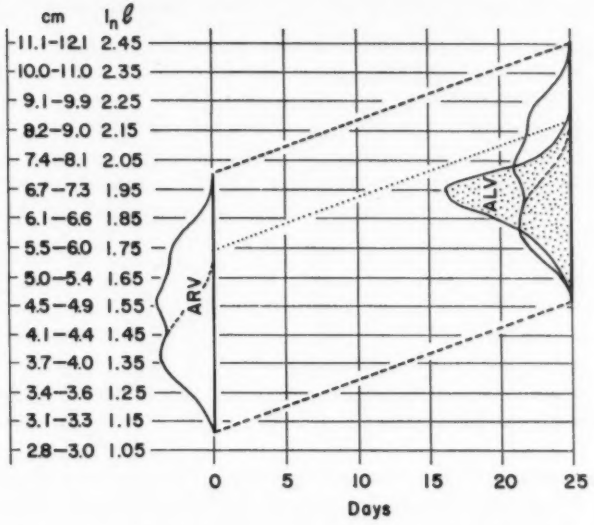

FIG. 6. Comparison of length frequency curves of ARV and ALV marked groups. See text for explanation.

having a slope of 0.0186 per day, and the length frequency curve representing ARV fish is extrapolated along this slope and superimposed on that of the ALV fish. From this comparison it would appear that the larger ARV individuals were not present in the population during the ALV marking.

Marked ARV fish appeared in small numbers among the samples taken at Nalau Pass for the ALV marking (Table III). During this time, and subsequently until June 12, the waters of Fitz Hugh Sound were methodically searched for schools of pink salmon. None was found except in the vicinity of Nalau Pass. It was evident that a very large number of the 1961 brood year was present in Nalau Pass during the first few days of June. Either this accumulation represented a high proportion of the surviving 1961 brood year or substantial numbers had migrated seaward by some route which was not observed. The first proposition is considered more likely than the second.

Daily examinations and numbers of ARV marks found during this period are presented in Table III, and the hypothesis of homogeneity is examined. There is no apparent trend in time of deviations from the average incidence of marks and the resulting $\chi^2 = 10.5$ might be exceeded in more than 1 in 20 trials. Thus it is concluded that the smaller ARV-marked fish were thoroughly mixed in the population during the ALV marking.

While the 190 ARV-marked fish which were recovered were not measured, nothing unusual about the size was noticed. From samples preserved during the first 10 days of June, five marked fish were measured, and all fell within the major frequency classification 6.7–7.3 cm. All of these observations lend support

TABLE III. Observations on ARV-marked pink salmon during the second (ALV) marking in Nalau Pass, British Columbia, 1962.

Date	No. of fish observed		Expected ARV	Deviations (E–O)
	Unmarked	ARV		
June 2	20,830	29	34.6	−5.6
" 3	23,173	42	38.5	+3.5
" 4	27,435	57	45.6	+11.4
" 5	24,569	26	40.9	−14.9
" 6	18,260	36	30.4	+5.6
Total:	114,267	190	190.0	0

$\chi^2 = 10.5$, d.f. = 5, $0.10 > P > 0.05$

to the hypothesis that the smaller ARV fish were present and thoroughly mixed with the populations present in Nalau Pass during the second marking period. The larger ARV-marked fish, it is assumed, had previously migrated from the enclosed waters of the study area.

To permit an estimate of the stock of ARV marks available at the time of ALV marking a dotted line has been added in Fig. 6 to the length frequency curve of the ARV population which approximates a distribution similar to that of the ALV group. This treatment divides the area of the curve into about 50% "small" and 50% "large" ARV fish.

The pertinent values for future computations are, then:

1. 181,966 ARV marks were released during May 5–14. These are separated into two main groups by use of length frequency and growth rate:
   a. Smaller fish, 50% of the total, are considered to be of mixed Kwatna and Bella Coola River origin. Other smaller Burke Channel and upper Dean Channel stocks may be involved.
   b. Larger fish, 50% of the total, are termed local Fisher–Fitz Hugh Sound stocks. These stocks are known to be of relatively low abundance, therefore a relatively large proportion of their number may have been marked.

2. 112,858 marked ALV were released during June 2–6. These are considered to consist primarily of Bella Coola River and Kwatna stocks and are identified with the "small" component of the ARV marking.

3. The time period between 50% release dates of the two markings is 25 days.

4. 190 ARV marks were recovered during the examination of 114,267 fish at the time of the second marking.

ADULT POPULATION RETURNING

The 1963 commercial fishing season (when the 1961 brood was returning to spawn) was interrupted and effectively closed by a labour dispute during most of July. Prior to July 10, only small and scattered catches were reported. Fishing recommenced on August 5. Throughout Statistical Areas 7 and 8 (Fig. 7) 5 days, fishing was allowed August 5–9. This was followed by a 4-day fishing week, August 12–15, and thereafter 3 days' fishing per week was allowed until the fall closure on September 19.

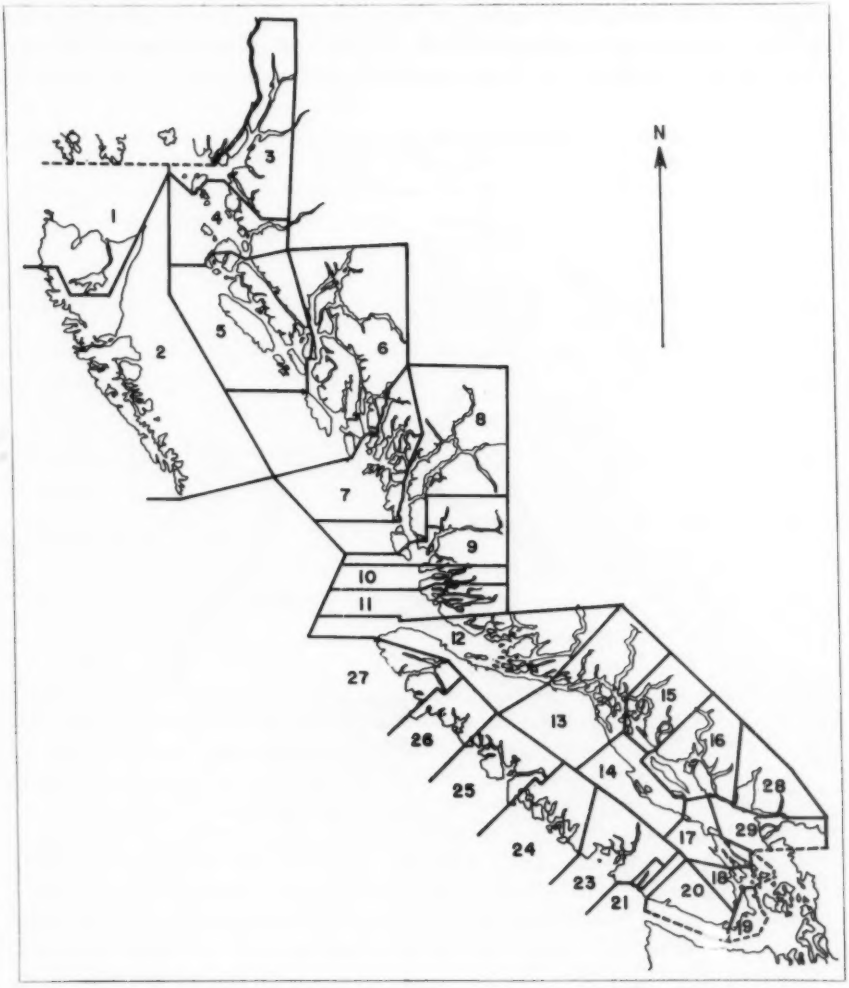

FIG. 7. Division of British Columbia coastal area into statistical areas.

Within Area 8, the lower portions of Dean and Burke Channels were closed to fishing the entire season and two special areas, North Bentinck Arm and the area surrounding the Koeye River estuary in Fitz Hugh Sound were closed after August 18. These gross features of the 1963 fishing restrictions are shown in Fig. 8. In Area 7 and in Fisher Channel–Fitz Hugh Sound both purse-seines and gill-nets operated, the seines accounting for the bulk of the catch. In upper Burke and Dean Channels only gill-nets were allowed. Catches in Dean Channel were insignificant, amounting to less than 2000 fish. The Burke Channel–Bella Coola gillnet fishery was effectively restricted to approximately 3 days' fishing during the August 5–9 period as the volume of catch exceeded facilities available for transportation to cannery sites, resulting in a voluntary restricted catch period.

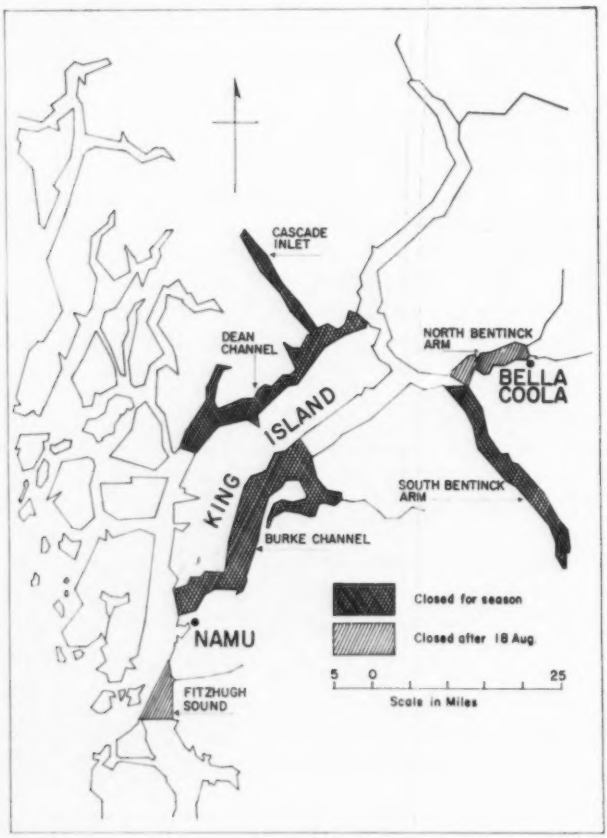

FIG. 8. Area and time fishing restrictions within Statistical Area 8 in 1963.

Official catch statistics are available only for the broad Statistical Areas as shown in Fig. 7, however, local Department of Fisheries Officers were able to estimate the catches originating from the Burke Channel–Bella Coola gillnet area by daily radio contacts with the industry collecting boats. This information was utilized to prepare the estimates of 1963 pink salmon catches as presented in Table IV. Using the average catch per day's fishing as an index to the numbers of fish available it is noted that during the first three August fishing periods the numbers of fish available probably remained approximately the same in Area 7 during the first 2 weeks, then fell. In Fisher Channel–Fitz Hugh Sound availability declined each succeeding week of the fishery. In Burke Channel, availability remained fairly constant during the first two periods but fell precipitously the third week. During weeks I and II the fishery was concentrated

TABLE IV. Estimated catches, in 1000s of fish, of pink salmon and average catch per day's fishing (parentheses) during 1963 fishing season, central British Columbia.

Area	Fishing periods					
	June 24–July 10	Aug. 5–Aug. 9 Week I	Aug. 12–Aug. 15 Week II	Aug. 19–Aug. 21 Week III	Aug. 26–Sep. 18	Total
Statistical Area 7	6.6	173.4	138.0	57.2	25.6	400.8
		(34.7)	(34.5)	(18.9)		
Fisher Channel–Fitz Hugh	4.4.	651.9	336.8	123.4	39.5	1,156.0
Sound		(130.4)	(84.2)	(40.7)		
Burke Channel–Bella Coola	0.3	346.7	444.7	44.5	11.8	848.0
		(114.4)	(111.1)	(14.7)		
Total:	11.3	1,172.0	919.5	225.1	76.9	2,404.8

in North Bentinck Arm, presumably fishing on the accumulating Bella Coola run. It is assumed that the apparent decline in abundance was caused, in part, by the closure of North Bentinck Arm to fishing during week III and in part to the entrance of the run into the Bella Coola River.

During the 3-week period August 5–24, samples of catches landed at Namu and Vancouver were examined for marked fish. In total, 511,400 fish were examined and 256 ARV and 349 ALV marks were found. During these 3 weeks, approximately 92% of the Area 7, 96% of the Fisher Channel–Fitz Hugh Sound, and 99% of the Burke Channel catches were landed. The distribution of sampling and marks found is summarized in Table V. In total, approximately 6.8% of Area 7, 21.5% of Fisher Channel–Fitz Hugh Sound, and 27.7% of Burke Channel–Bella Coola catches were examined.

TABLE V. Numbers of pink salmon examined (in 1000s of pieces) and marks found, central British Columbia 1963 commercial catch, 1961 brood-year pink salmon.

Area		Fishing periods			Total
		Aug. 5–9 Week I	Aug. 12–15 Week II	Aug. 19–21 Week III	
Area 7	No. examined		18.0	9.4	27.4
	ARV		17	6	23
	ALV		6	5	11
Fisher Channel–Fitz Hugh Sound	No. examined	115.4	96.1	37.6	249.1
	ARV	68	88	46	202
	ALV	73	74	44	191
Burke Channel	No. examined	63.5	156.6	14.8	234.9
	ARV	4	20	7	31
	ALV	43	95	9	147
Total:	No. examined	178.9	270.7	61.8	511.4
	ARV	72	125	59	256
	ALV	116	175	58	349

THE SPAWNING POPULATIONS

Area 8 contains several small spawning populations in addition to the large Bella Coola River run. According to gross spawning-ground population estimates made available by the Department of Fisheries, the Bella Coola River stock usually accounts for more than 90% of the total spawning populations within the area. In 1963, crude estimates of the spawning runs were again made available and indicate that, in 1963, about 75% of the Area 8 escapement may have utilized the Bella Coola system. A great majority of these utilized the spawning grounds of the Atnarko River (Table VI).

The Atnarko River is a clear-water stream of relatively stable flow which joins with the glacial Talchako about 30 miles east of Bella Coola to form the Bella Coola River. Spawning in the main Bella Coola River by pink salmon has not been demonstrated, but remains a possibility. In the Atnarko, pink salmon generally utilize about 20 miles of stream and special efforts were directed in 1963 to estimate this spawning population.

During the period September 4–16, 5799 pink salmon were captured by seine, tagged, and released at the mouth of the Atnarko River. Subsequently, 85,935 dead pink salmon were examined on the spawning grounds. This examination was terminated on October 2 when very few live pink salmon remained

TABLE VI. Approximate distribution of Area 8 pink salmon spawning stocks in 1963.

Subarea	Estimate[a]	Per cent
Bella Coola	400,000	75
South Bentinck Arm	3,000	>1
Burke Channel	52,000	8
Dean Channel	31,000	6
Fisher Channel	1,000	<1
Fitz Hugh Sound	50,000	9
Total:	537,000	

[a]Based on gross estimates supplied by Department of Fisheries plus the Bella Coola estimate of this paper (see text).

in the stream. Estimates of the spawning population, derived from the recovery of tags in the sample examined, are presented in Table VII.

The sum of the estimated male and female populations (443,352) is less than the estimate derived from the total statistics (508,507). This is most likely an indication that the sexes were neither tagged nor subsequently sampled in proportion to their numbers in the spawning populations (Ricker, 1958).

The sex ratio of the tagged population was 77 ♂:23 ♀ (3:1). This ratio reflects the well-known tendency of the males, due to morphic changes of the jaws and teeth accompanying sexual maturity, to become entangled in the seine while a portion of the females always seems to escape under the lead line.

Sampling of dead salmon on the spawning grounds indicated a 42 ♂:58 ♀ (0.7:1) sex ratio. Here again, it is well known that the females tend to guard their nests until they die, while the males are displaced down stream after spawning but yet alive. Thus the female population becomes more available to sampling when dead fish are utilized. For these reasons the sum of the estimated

TABLE VII. Estimates of 1963 Atnarko River pink salmon spawning population as derived from tag and recapture method.

	Males	Females	Total
Tagged	4,459	1,340	5,799
Sampled	35,941	49,994	85,935
Tags recovered	596	384	980
Population estimate	268,894	174,458	508,507
Sum of ♂ and ♀ estimates:		443,352	

male and female spawning populations is a more appropriate estimate of escapement to the Atnarko River spawning grounds. Approximate 95% confidence limits were derived for this estimate as the sum of the limits for the male and female estimates (De Lury, eqn. 1.13, 1951) using t at the $\sqrt{.05}$ level of probability. The value of t at this level was obtained by graphic interpolation. The approximate limits are 420,000 and 469,000 fish.

Experience with other tag and recovery estimates of spawning pink salmon has revealed a tendency to overestimate the population because of tag losses due to a variety of causes. Fisheries Research Board studies (Vernon *et al.*, 1964) on the Glendale River, where tag and recovery estimates were compared with weir counts, indicated that population estimates derived from fish tagged in the estuary were 1.415 times the weir count. Where fish were seined and tagged in the stream at the lower limit of spawning, the estimate was 1.342 times the fence count. Where fish were trapped at the fence (a short distance above the seining site) and tagged proportionally to the daily numbers counted, the resulting estimate was 1.171 times the fence count. The situation for the Atnarko tagging most closely approximates the stream seining at Glendale, and the Atnarko estimate is corrected by "borrowing" the coefficient 1.342. Thus an "improved" estimate of the Atnarko River spawning population is approximately 330,000, or between the approximate 95% confidence limits 313,000 and 349,000 fish.

During the period September 18–22, 21 miles of the Atnarko River above its confluence with the Talchako was covered on foot and with the aid of a rubber raft to estimate the "standing" population of live fish. At this time spawning was in progress and the population had virtually completed its migration into the Atnarko River. The population of live fish was estimated at between 206,000 and 271,000. It was further estimated that 20–25% of the total population was dead. Thus the estimate of the total population by this means is between the extreme estimates 258,361 and 361,000 fish. These two independent estimates, carried out by different personnel and without exchange of information, are in close agreement.

The more refined estimate of the Atnarko spawning population, derived from the adjusted tagging and recovery data, of 330,000 fish is adopted. Spawning populations of other Bella Coola tributaries and of North Bentinck Arm amounted to about 59,000 fish according to gross estimates obtained from the Department of Fisheries. Altogether, a spawning escapement (in round numbers) of 400,000 (which may be in error as much as $\pm 10\%$) is estimated for North Bentinck Arm streams and is hereafter referred to as "Bella Coola" escapement. This estimate is used with the gross estimates provided by the Department of Fisheries to indicate the distribution of spawning populations within Area 8 as given in Table VI.

The fish seined and tagged at the mouth of the Atnarko River were closely examined for marks. Of the 5799 examined, 3 ALV marks were found. The marks recognized on post-spawning dead salmon, however, fall far short of the expected numbers. This discrepancy is considered to arise from a lack of close

inspection. After spawning the fins of these salmon were usually worn and broken, and only a very close inspection could reveal a genuine mark. The crews employed in pitching the dead fish were primarily interested in recovery of the more obvious tag and undoubtedly the greater portion of marked fish were not recognized. Of the 85,900 fish pitched only 5 ALV and 1 ARV were reported. This ratio of ALV:ARV, while not statistically significant, might be expected from the mark returns of the first 2 weeks of the Burke Channel gillnet fishery. The recoveries definitely indicated that Bella Coola fish were present in both marked populations.

ESTIMATES OF MORTALITY RATES

For a given number of marked pink salmon released as fry, the number returning as the adult population is determined by the natural mortality rate and the effect of marking on the natural mortality rate during the time period between release and return. The following notation is used:

N— denotes the number of fish present in a population at any time.

t— denotes the time in days as measured from release ($t = 0$).

S_M— denotes the decimal fraction of the marked population which survive short-term effects of marking and

m— denotes the continuing effect of the mark on the day-to-day probabilities of death from natural causes, as denoted by

q— the instantaneous natural mortality rate.

These types of mortality resulting from marking are discussed by Parker *et al.* (1963).

Symbolically, these relationships are expressed by the equation

$$N_t = N_0 S_M e^{-mqt} \tag{1}$$

A two-stage marking experiment can theoretically yield the instantaneous mortality rate during the time period between first and second markings. For example, a population marked a is released at time $t = i$. A second population marked b is released at time $t = j$. Both populations are then assessed at time $t = k$. For population a

$$N_{ak} = N_{ai} S_{Ma} e^{-mq(k-i)} \tag{2}$$

and for population b

$$N_{bk} = N_{bj} S_{Mb} e^{-mq(k-j)} \tag{3}$$

With the assumption that both populations are subject to the same natural mortality rates during the period i to k, equations (2) and (3) used as simultaneous equations will yield the instantaneous rate of natural mortality for the time period i to j. Thus by dividing equation (2) by equation (3) and transposing terms

$$e^{-mq(j-i)} = \frac{N_{ak}N_{bj}S_{Mb}}{N_{bk}N_{ai}S_{Ma}} \qquad (4)$$

The solution of equation (4) depends upon the values of the *ratios* N_{ak}/N_{bk}, N_{bj}/N_{ai}, and S_{Mb}/S_{Ma}. The first ratio, N_{ak}/N_{bk} might be accurately estimated from sampling the total population if the two marked populations are randomly dispersed within the total population and thus have probabilities of detection proportional to their actual abundance. In the present problem, catches were inspected for marked fish, however, it is suspected that the two marked popula-

TABLE VIII. Sample sizes and numbers of marks found in pink salmon catches and escapements, Burke Channel, 1963.

Sample	Number in sample (1000s)	Marks found	Incidence of mark (per 1000)
ARV:			
Fishery, Week I	63.5	4	0.06
Fishery, Week II	156.6	20	0.13
Fishery, Week III	14.8	7	0.47
Totals I, II, III	234.9	31	0.132
Totals I, II	220.1	24	0.109
[χ^2 I.II.III = 10.32, $0.01<P<0.02$]			
[χ^2 I.II = 2.69, $0.20<P<0.30$]			
ALV:			
Fishery, Week I	63.5	43	0.68
Fishery, Week II	156.6	95	0.61
Fishery, Week III	14.8	9	0.61
Atnarko River	5.8	3	0.51
Total:	240.7	150	0.62
[χ^2 = 1.95, $0.70<P<0.80$]			

tions were subjected to different rates of exploitation because of differences in timing and rates of travel. The assumption of proportional probabilities of detection is, therefore, not likely to be valid. In lieu of this condition it is necessary to estimate the total number of fish surviving to the adult returning stage for each marked group.

The ratio N_{bj}/N_{ai} (the numbers of marks released) may be known exactly from the number of ALV and ARV marks released. In the present case, however, there are complications in the interpretation of the number of ARV marks released, as will be discussed later.

The ratio S_{Mb}/S_{Ma} (Eqn. 2) will be considered next. Both lots for marking were captured, held, marked, and released in a similar manner. At release, bleeding had stopped and excised surfaces were covered with a membrane of scar tissue. No differences were apparent between the groups in this respect. On several occasions, mixed lots of marked and unmarked fish have been held for several days and little if any mortality attributable to marking per se has been observed after 12 hr. The ratio S_{Mb}/S_{Ma}, for these markings, is considered to be approximately equal to 1 and therefore eliminated in subsequent calculations.

The value of m, the marking coefficient for long-term effect on the prevailing mortality rate, is next considered. An analysis of mark returns from several pink salmon marking experiments and the selectivity of a predator for marked individuals under experimental conditions has been presented (Parker *et al.*, 1963). The results of the 1960 Hook Nose Creek brood-year marking (Parker, 1964; Table IX) yield a value $m = 1.37$. The average of all information on this coefficient is $m = 1.38$. This value will be used in subsequent calculations.

For a first approximation of the instantaneous mortality rate (q) the total numbers of marked fish released and the numbers of marked fish found in samples of the adult catch may be used. Thus, where the time period between dates on which 50% of each population was released, $k-i = 25$ days.

$$\left.\begin{aligned} N_{ak} &= 256 \text{ ARV} \\ N_{bk} &= 349 \text{ ALV} \end{aligned}\right\} \text{adult return ratio}$$

$$\left.\begin{aligned} N_{bj} &= 112{,}858 \text{ ALV} \\ N_{ai} &= 181{,}966 \text{ ARV} \end{aligned}\right\} \text{marks released ratio}$$

With these values the solution of equation (4) gives $q = 0.0228$. The validity of this solution depends mainly upon the assumption of equal rates of inspection of both marked populations as returning adults. That this assumption is not likely to be valid may be shown from a study of various rates of incidence of ARV and ALV marks in catches classified by week and by area of fishing. These are compared graphically in Fig. 9.

TABLE IX. Estimations of the numbers of ARV and ALV marked pink salmon returning as matures (catches + escapements) to the Burke Channel–Bella Coola Area, 1963.

Estimate	Stock unit		Total
	Bella Coola	Burke Channel	
Catch	791,700	56,300	848,000
Escapement	400,000	55,000	455,000
Total:	1,191,700	111,300	1,303,000
Mean estimate			
ARV/1000	0.11	0.47	...
Total ARV	131	52	183 (N_{ak})
ALV/1000	0.62	0.62	...
Total ALV	739	69	808 (N_{bk})
Lower estimate			
ARV/1000	0.07	0.11	...
Total ARV	83	12	95 (N_{ak})
ALV/1000	0.52	0.52	...
Total ALV	620	58	678 (N_b)
Upper estimate			
ARV/1000	0.16	0.83	...
Total ARV	191	92	283 (N_{ak})
ALV/1000	0.72	0.72	...
Total ALV	858	80	938 (N_{bk})
N_{ak}/N_{bk} =	0.23, (mean estimate)		
	0.42 (max. estimate)		
	0.10 (min. estimate)		

Consider first the ARV returns. The incidence of ARV marks in Fisher Channel–Fitz Hugh Sound catches was much greater than in Burke Channel–Bella Coola catches, indicating (as previously concluded) that both Fisher Channel–Fitz Hugh Sound and Burke Channel–Bella Coola stocks were involved in the first marking, and a larger proportion of the Fisher Channel–Fitz Hugh Sound stock was marked than of the Burke Channel–Bella Coola stock. Furthermore, the increase in ARV/1000 as the season progressed indicates

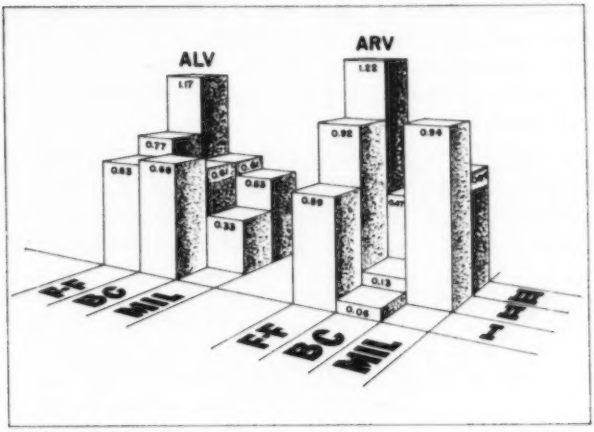

FIG. 9. Comparison of ARV and ALV per 1000 fish classified by area and week of recovery. See text for explanation.

that either the marked Fisher Channel–Fitz Hugh Sound fish appeared late in the run or that they became progressively less diluted by unmarked members of the larger Bella Coola stock.

Considering the ALV returns, the Burke Channel samples indicate a rather constant proportion of ALV marks throughout the season. The Fisher–Fitz Hugh samples, in contrast, indicate an initial ALV incidence similar to that in Burke Channel, but as the season advanced the fraction of ALV marks almost doubled.

These results are interpreted as indicating that the Burke Channel–Bella Coola stocks may be divided roughly into two groups. Approximately equal percentages of each group were marked ALV, while unequal percentages were marked ARV. A much higher proportion of Fisher Channel–Fitz Hugh Sound stocks were marked at the first marking (ARV), and to a lesser degree this is true of the second marking (ALV). Since Burke Channel–Bella Coola stocks moved through the Fisher Channel–Fitz Hugh Sound fishery and became unavailable while the local stocks remained available, the latter were undoubtedly fished at a higher rate by that fishery. The Burke Channel–Bella Coola stocks were subjected, in addition, to the Burke Channel–Bella Coola gillnet fishery but only by coincidence would the total rates of exploitation on these stocks be equal to that of the local Fisher Channel–Fitz Hugh Sound stock. The results of the 1960 brood-year study (Parker, 1964) indicated that the total rate of exploitation on Burke Channel–Bella Coola stocks would be much less than that on Fisher Channel fish. This type of difference would result in the recovery of too many ARV marks in relation to the recovery of ALV, in turn resulting in the underestimation of q. Thus the first approximation, $q = 0.0228$, is too low.

It is therefore necessary to isolate stocks and adjust releases and returns to some common rate of exploitation. This will be attempted for the Burke Channel–Bella Coola stocks. It is assumed that prior to entering Burke Channel, all component stocks spawning in Burke Channel–Bella Coola streams were subjected to the same rate of exploitation.

It has been demonstrated that the population of ARV-marked fish included two types, separated as 50% small and 50% large on the basis of growth rate and length–frequency data. It was suggested that the small component was composed of pink salmon originating in Burke Channel–Bella Coola streams, which subsequently became available for marking (ALV) at Nalau Pass. Thus the estimate of the ratio N_{bj}/N_{ai} is (from Table I),

$$(112{,}858)/[0.5(181{,}966)] = 1.24.$$

Sample sizes and numbers of ARV and ALV marks found in Burke Channel are recorded in Table VIII. The χ^2 tests indicate a significant dissimilarity between ARV/1000 during weeks I + II and week III samples from the fishery. During weeks I and II (accepting the hypothesis of homogeneity) it is estimated that 0.11/1000 fish bore the ARV mark. During week III, however, the ratio increased to an estimated 0.47/1000. Changes in incidence of ALV marks were not significant, and the average, 0.62 ALV/1000, is therefore assumed to be applicable for both catches and the escapements of Burke Channel–Bella Coola stocks. The differences in the returns of ARV marks are a strong indication that more than one stock of pink salmon was involved in the Burke Channel–Bella Coola fishery.

From the relatively constant incidence of ALV marks in both catches and escapement to the Atnarko it may be postulated that (assuming there are only two Burke Channel–Bella Coola stocks involved) both stocks were proportionately represented in the population present in Nalau Pass at the second marking. At the first marking at Fogner Bay, however, the Bella Coola stock was not represented as well as the "other" stock, i.e. a greater portion of the other stock was marked. During fishing weeks I and II the Bella Coola stock undoubtedly provided the main portion of the catches and the average 0.11 ARV/1000 is mainly due to the mark incidence of that stock. During week III, North Bentinck Arm was closed to fishing and the catches thereafter contained a much larger proportion of the other stock of which a much higher proportion were marked, thus increasing the observed incidence of ARV to 0.47/1000.

There are no observations which directly identify the other stock. From the distribution and apparent movements of small fish during 1962 it is suspected that Kwatna River pink salmon were, to a large degree, involved. The Kwatna River stock is the only non Bella Coola stock of significant size in the Burke Channel area. It is necessary at this point to make several additional assumptions:

a. That the Atnarko River stock and other stocks native to streams either tributary to the Bella Coola River or entering North Bentinck Arm can be considered as a single unit, with characteristic incidence of ARV and ALV marks.

b. That escapement of the non Bella Coola unit, the other stock, is represented by the gross estimate of 55,000 for the Kwatna River and other Burke Channel–South Bentinck Arm spawning populations (Department of Fisheries estimate).

c. That the Burke Channel–North Bentinck Arm catches during fishing weeks I and II were virtually all attributable to the Bella Coola unit.

d. That the Burke Channel catch during and after fishing week III was virtually all attributable to the non Bella Coola unit.

Assumptions (c) and (d) are certainly not strictly true. However, a more accurate separation cannot be made with the available information, and the assumptions have the effect of assigning an ARV/1000 ratio that is too high to the Bella Coola unit and somewhat too low to the non Bella Coola component. These assumptions allow the estimation of ARV- and ALV-marked fish returning to Burke Channel, as presented in Table IX.

In Table IX, approximate 0.95 confidence intervals have been applied to the estimated numbers of marks returning. The estimates of the ratio N_{ak}/N_{bk} are given as mean, upper, and lower limits. These limits were obtained by combining the upper limit of N_{ak} with the lower limit of N_{bk} and vice versa. The statistical probability of obtaining these limits would be $1/20^2$ or 1/400, not very likely to occur. On the other hand, several assumptions have been made, and the error thus introduced cannot be fully evaluated. The limits of N_{ak}/N_{bk} are proposed as sufficient to encompass the effects of all assumptive errors which may have been made.

Accordingly, three estimates of instantaneous natural mortality rate for the time period between markings are offered. These are (from Eqn 4), for marked fish,

lower limit:

$$e^{-25\,mq} = (1.24)\,(0.42),\ mq = 0.02608$$

mean estimate:

$$e^{-25\,mq} = (1.24)\,(0.23),\ mq = 0.05016$$

upper limit:

$$e^{-25\,mq} = (1.24)\,(0.10),\ mq = 0.08340.$$

Substituting the value 1.38 for m, the value of q is estimated to lie between the limits 0.0189 and 0.0604 and the most likely value is $q \approx 0.0363$.

These estimates apply to a 25-day period which is a later portion of a period of about 40 days spent in the enclosed waters of Burke Channel and Fitz Hugh Sound before migration into the open waters of Queen Charlotte Sound. The initial 10 days (occurring previous to the above 25-day period) during which the pink salmon are at their smallest size, may be assumed to be at least equally as hazardous to survival. The apparent population remained in or adjacent to Nalau Pass for about 5 days after the central release date (June 4) of the second (ALV) marking. Therefore it is reasonable that these rates be extended to include the entire 40-day period and considered as conservative estimates of the mortality rate during that period. Thus 40 $q \approx 1.454$, or between the limits 0.756 and 2.417. Thus it is conservatively estimated that between 53% and 91%, with the most probable value of 77%, of the entering fry population died during the initial 40-day period in enclosed waters.

In order to obtain an estimate of the total sea mortality of the Burke Channel–Bella Coola stocks it is necessary to estimate both the number of fry entering the sea and the total number of fish returning in the adult population.

Let N_t represent the number of fish in this population at any time t.

U,M used as subscripts denote unmarked and marked members, respectively.

i denotes the central date of first marking, the ARV group, and

j denotes the average date of second marking (ALV). Again $j-i = 25$ days.

For the unmarked group,

$$N_{jU} = N_{iU}e^{-q(j-i)} \tag{5}$$

However, the number of Burke Channel–Bella Coola fry marked ARV was estimated to be only 0.5 of the total released. Therefore, assuming that all of the ARV marks recovered at the ALV marking ($t = j$) were Burke Channel–Bella Coola stock,

$$N_{jM} = 0.5N_{iM}e^{-mq(j-i)} \tag{6}$$

Dividing equation (5) by equation (6) and transposing terms,

$$N_{iU} = [N_{jU}/N_{jM}]0.5N_{iM}e^{-q(j-i)(m-1)} \tag{7}$$

The size of the entering fry population at $t = 0$ is estimated as

$$N_{0U} = N_{iU}e^{-q(i-0)} \tag{8}$$

Substituting (7) into (8),

$$N_{0U} = [N_{jU}/N_{jM}]0.5N_{iM}e^{-q[i-(j-i)(m-1)]} \tag{9}$$

Using the "best" estimates of the various terms in equation (9) (from Tables I, III, and text),

$$N_{jU}/N_{jM} = 114{,}267/190 = 601.4$$

$$N_{iM} = 181{,}966$$

$$q = 0.0363$$

and $i = 10$, $j = 35$, $m = 1.38$, the entering fry population,

$$N_{0U} \approx 55.7 \times 10^6.$$

Confidence intervals have been estimated for some of the terms of equation (9) as follows:

	N_{jU}/N_{jM}	q
Upper limit	114,267/165 = 692.5	0.0604
Lower limit	114,267/219 = 521.8	0.0189

By following the limit values, extreme estimates of the entering fry population are estimated as 64.9×10^6 (upper) and 47.9×10^6 (lower). The various estimates obtainable are presented in Table X.

Information for separating Area 7 and Fisher Channel–Fitz Hugh Sound catches directly into Burke Channel–Bella Coola and non Burke Channel–Bella Coola components is not available. In general, it can be stated that Fisher Channel–Fitz Hugh Sound catches contained large numbers of Burke Channel–Bella Coola stocks simply from the argument that spawning ground escapements to other areas, in aggregate, formed a minor portion (approximately 16%) of the total escapement. This is not to say, however, that the Burke Channel–Bella Coola stocks provided 84% of the catch, because the rate of exploitation on

TABLE X. Estimates of the number of pink salmon fry entering Burke Channel–Bella Coola obtained from equation 9 using 0.95 confidence limits of terms (see text).

		Values of $e^{-q[(i-1)(m-1)]}$		
		Upper	Mean	Lower
Values of $[N_{jU}/N_{jM}]0.5N_{iM}$		1.030	1.018	1.009
Upper	63.0×10^6	64.9×10^6	64.1×10^6	63.6×10^6
Mean	54.7×10^6	56.3×10^6	55.7×10^6	55.2×10^6
Lower	47.5×10^6	48.9×10^6	48.4×10^6	47.9×10^6

the other components may have been different than that on the Burke Channel–Bella Coola stocks. As an approximation, it is suggested that the Burke Channel–Bella Coola stocks may have supplied 90% of the Fisher Channel–Fitz Hugh Sound catch taken during the fishing periods up to the end of week III and none of the remainder. Using the spawning escapement estimates given in Table VI and catches from Table IV, the Fisher Channel–Fitz Hugh Sound fishery would have taken approximately 151,200 fish from local and Dean Channel stocks with the rate of exploitation $u \approx 0.60$. The same fishery would have taken 1,004,800 fish from Burke Channel stocks, $u \approx 0.43$. The average rate $u \approx 0.60$ is probably too high for Dean Channel stocks (on the basis of 1960 brood year study) but may be a close approximation for the relatively large Koeye River stock which was protected by a sanctuary area after August 19. There are some minor stocks which are subject to much higher rates of exploitation, e.g. Hook Nose Creek. With these estimates, a catch of 1,004,800 Burke Channel fish by the Fisher Channel–Fitz Hugh Sound fishery is a reasonable approximation.

Catches from Area 7 also contained large numbers of fish en route to Area 8 streams. The incidence of ARV marks was, however, proportionately higher than that of ALV marks when compared to Area 8. This is interpreted to indicate that a higher proportion of local Fisher Channel–Fitz Hugh Sound stocks than of Burke Channel–Bella Coola stocks passed through Area 7. These clues provide a means of estimating the Burke Channel–Bella Coola contribution to the Area 7 catches.

Samples of Area 7 catches were examined only during fishing weeks II and III. The resulting data are presented in Table XI. It is noted that differences between weeks regarding incidence of marks are not significant. Homogeneity is assumed. A chi-square test for homogeneity with Burke Channel–Bella Coola stocks characterized by 0.62 ALV/1000 discloses no significant differences ($\chi^2 = 1.33$, $p \approx 0.25$) so it is possible to say, from these data, that a high proportion of Area 7 catch during weeks II and III may have been of Burke Channel–Bella Coola origin. The fraction of Burke Channel fish is estimated by the fraction $0.40/0.62 = 0.65$. By their timing, Burke Channel–Bella Coola fish may have formed even a larger proportion of catches during and prior to week I, and after week III the catches must have contained a much larger proportion of local stocks. For the present purposes, an estimate, considered to be too low, may be made by taking 65% of catches prior to and including week III. This is 266,400 fish. Following 0.95 confidence limits, extreme values are 78,800–375,200 fish.

The mean estimates of Burke Channel stock contributions and escapements are given in Table XII which includes estimates of rates of exploitation. The latter cannot be computed for the Area 7 fishery because the proportion of the entire Burke Channel–Bella Coola stock available to the Area 7 fishery is not known. The combination of successive fisheries, however, resulted in an estimated total rate of exploitation, $u = 0.85$.

TABLE XI. Samples obtained from Area 7 pink salmon catches and incidence of marks in 1963.

	Fishing period					
	June 24–July 10	Week I	Week II	Week III	Aug. 26–Sept. 18	Total
Catch	6.6	173.4	138.0	57.2	25.6	400.8
Sample	0	0	18.0	9.4	0	27.4
ARV (number)	...	...	17	6	...	23
ARV/1000	...	...	0.94	0.64	...	0.84
ALV (number)	...	...	6	5	...	11
ALV/1000	...	...	0.33	0.53	...	0.40

χ^2 ARV II.III = 0.596, $P \approx 0.42$

χ^2 ALV II.III = 0.499, $P \approx 0.51$

0.95 C.I. ARV/1000 $\approx \underline{0.53}$–$\overline{1.26}$

0.95 C.I. ALV/1000 $\approx \underline{0.20}$–$\overline{0.72}$

TABLE XII. Estimated catches of Burke Channel–Bella Coola pink salmon and rates of exploitation by areas in 1963.

	Best estimate	Stock available	Rate of exploitation
Area 7 catch	266,400	?	0.09
Fisher Channel–Fitz Hugh Sound catch	1,004,800	2,646,500	0.38
Burke Channel–Bella Coola catch	1,191,700	1,641,700	0.73
Spawning escapement	450,000	...	...
Total:	2,912,900	...	0.846

The resulting estimate of the total return of Burke Channel–Bella Coola stocks is a summation of various estimates. The Area 7 catch may be considerably in error, but forms a minor portion of the total calculated return. The Fisher Channel–Fitz Hugh Sound catch, while on a firmer basis, also may be in error. Considering the arguments already presented, error cannot be considered serious. The Burke Channel–Bella Coola catch is simply the sum of catches reported by the fishing industry and may be considered as a relatively accurate estimate. The spawning ground escapement estimate, while less accurate, again

forms a small proportion of the total. Not included in the total are estimates of natural mortality during the fishing period or deaths due to the fishery that did not enter the reported catch. No information on the possible magnitude of these types of losses is available. Accepting the estimate of return as 2,912,000, survival(S) from fry to adult is estimated as 0.052. Using the extreme estimates of fry population size, the real value of S is likely to be included in the limits 0.046–0.058. Compared to the estimate S = 0.22 for 1960 brood year Hook Nose Creek pink salmon, the sea survival during 1962–63 was undoubtedly much lower. This, however, is consistent with the known general situation, for the return of 1960 brood-year pink salmon produced a record catch of over 12,000,000 fish in the study area.

The estimate of S = 0.052 is equivalent to a total instantaneous natural mortality rate (Σq) of 2.950 for the (approximate) 450-day period of marine residence. During the first 40 days, 40 $q \approx 1.452$ leaving 1.503 to apply for the total remaining time of approximately 410 days. In the latter period, the estimate of average $q \approx 0.0037$. This value, compared to $q \approx 0.0363$ the initial 40-day period rate on a per day basis, is in a different order of magnitude.

By combining the upper and lower limit estimates of early and total mortality rates various estimates of instantaneous mortality rates (q) for early coastal and oceanic stages of life can be made. These are compared in Table XIII. Even using extreme values in improbable combinations, the instantaneous mortality rate during the early coastal period is several times that of the associated oceanic rate.

The following rounded approximations have been assigned to the 1961 brood-year Burke Channel–Bella Coola pink salmon population:

Fry entering sea, late April 1962	55.7	million
Fraction dying, fry to migrant stage, June 1962	0.77	
Number of migrants emigrating from Fitz Hugh Sound	13	million
Fraction dying, smolt to adult return	0.78	
Number of adults returning, August 1962	2.9	million
Rate of exploitation	0.85	
Spawning escapement	0.45	million

TABLE XIII. Combination of upper and lower limit values of total and early coastal mortality rates to provide maximum, most likely, and minimum differences between the two rates. 1961 brood year, Burke Channel–Bella Coola pink salmon.

Difference oceanic–coastal	Total sea instantaneous mortality rate	Coastal 40 q	Oceanic q	Coastal q	Ratio oceanic–coastal
Maximum	2.845	2.416	0.0011	0.0604	55:1
Mean	2.950	1.452	0.0037	0.0363	10:1
Minimum	3.080	0.756	0.0057	0.0189	3:1

DISCUSSION

The assumptions necessary to the calculation of these estimates preclude placing great emphasis upon the "mean" values, which, after all, are better described as "most probable" values as determined by statistics and judgment. They may have a usefulness as indicators of magnitudes of natural mortality. It cannot be doubted that the relatively short initial coastal period of life was critical to the numerical strength of the adult return. During this short period of time, approximately 40 days, as large a fraction of the fish present at the start of the period died from natural causes as died during the succeeding 14 months in the sea.

In an earlier paper (Parker, 1962b) it was deduced that the monthly instantaneous rate of natural mortality of Pacific salmon, for the period of sea life away from the coast, i.e. oceanic, was $30\,q \approx 0.027$. It has been estimated above, that for the 1961 Burke Channel brood year $30\,q \approx 0.110$ for the final $13\frac{2}{3}$ months of sea life. These seemingly different results are actually compatible, for it is only necessary to extend the initial time period termed "coastal" to a total of $2\frac{1}{2}$ months to reduce the estimate of "oceanic" $30\,q \approx 0.024$. Fish leaving Fitz Hugh Sound are not yet away from the coast; in fact they have entered an area containing dense populations of potentially predacious species. This open coastal zone has not yet been studied in respect to the survival of pink salmon populations.

In addition, the mortality rate for the early period of sea life was based on the final 25 days in enclosed waters and then extrapolated to include the earlier period when fry first enter the estuary. This extrapolation may have seriously underestimated the initial mortality rate which in turn may have resulted in overestimating the remainder, i.e. ocean mortality rate. Thus the two approaches do not necessarily lead to incompatible results.

The main value resulting from this study is that the distribution of marine mortality of Bella Coola pink salmon is better understood. It is appreciated that stocks in any given area cannot be assumed to be randomly mixed. Even within a stock, fish are not randomly distributed in respect to size. Various stocks may each be subject to a particular rate of exploitation differing from that of any other. Precise interpretation of marking and sample recovery data is extremely difficult under these conditions. A new approach to the mortality question which circumvents these difficulties is needed. Nevertheless, the presented approximations may be quite useful as indicators of some of the major features of the vital statistics of pink salmon populations.

ACKNOWLEDGMENTS

The data presented in this paper were obtained through the faithful execution of field assignments by competent technicians. It is a pleasure to acknowledge Messrs Ralph C. Wilson, Kurt Mueller, and W. Neave in this regard. The analysis of the data and the written report received the excellent

criticisms of Dr Peter A. Larkin, Dr M. P. Shepard, Mr F. C. Withler, and Mr K. Radway Allen, all of the Biological Station, Nanaimo.

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Alexander's Method of Determining Swimbladder Volumes Modified for Living Physoclist Fish[1,2]

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ABSTRACT

A method to determine the swimbladder volume of living physoclists from its change in volume with change in applied pressure once the gas has been compressed sufficiently to remove the constraint of the swimbladder walls is given. The density of the fish at test depth was calculated from its mass, the seawater density, and the increase in volume of the fish with decrease in pressure from test depth to that causing neutral buoyancy.

INTRODUCTION

The method given by Alexander (1959a) allows the swimbladder volume of living, lightly-anaesthetised physostomes to be determined from measurements of the change in volume with increases in pressure of the swimbladder gas *in situ* and the volume change of the same mass of gas after part of it has been expelled from the swimbladder by a sharp reduction in pressure. Provided sufficient gas is expelled from the swimbladder all compression by the swimbladder walls is removed and this "unconstrained gas" obeys Boyle's Law so that its total volume at test depth may be calculated from its known change in volume with pressure. As the difference in volume of the unconstrained gas and of the gas still entirely within the swimbladder at zero applied pressure is known the volume of swimbladder gas can be found.

In physoclists gas cannot be expelled from the swimbladder by reducing the pressure but it can be freed from constraint due to the swimbladder or body walls while still inside the fish if sufficiently compressed by pressure applied externally. The applied pressure is sufficient to remove constraint when a plot of volume against the reciprocal of total pressure yields a straight line. From the change in volume of this unconstrained gas its total volume at 0 applied pressure may be calculated. The swimbladder volume at test depth is less than this by an amount shown on the same graph and so can be determined. This method, unlike that of Alexander (1959b), can be used for physoclists having an excess internal swimbladder gas pressure since it does not require that the same total volume at manometer 0 be obtained from the volume change between 0 and 6 cm Hg and from that between 0 and 18 cm Hg applied pressure.

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[1]Received for publication June 4, 1965.

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J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.

METHOD

The method was tested using "harbour" pollock, *Pollachius virens*, adjusted to a depth of 36 cm, the same depth as the test flask. The living fish was tested in sea water in a closed system similar to that described by Alexander (1959a) or Brawn (1962) where changes in volume with pressure are shown as movements of the seawater meniscus along a horizontal, calibrated capillary tube. It was modified by clamping the 6-litre, ring-necked test flask to the rest of the apparatus and holding down its top with a weighted sling to contain the increased internal pressure.

The fish was allowed to swim into the flask then anaesthetised with MS 222. The meniscus positions at increased applied pressures from 0 to 42 cm Hg in 6-cm Hg steps and after return to 0 were then recorded. This series of readings was sufficient to allow swimbladder volume to be calculated.

To determine body density and volume the fish was subjected to a slow decrease in applied pressure and the pressure and meniscus position at which the fish attained neutral buoyancy were recorded. The fish was killed and weighed after removing surplus water from the skin, buccal cavity, and gill filaments, and drying 20 min at room temperature. The density of sea water in the test flask and atmospheric pressure were recorded.

RESULTS

For an unconstrained gas a plot of volume against the reciprocal of total pressure will yield a straight line. Thus when the meniscus positions, corrected for temperature change and apparatus distortion and expressed as distances from the position at an applied pressure of 42 cm Hg, are plotted against the reciprocal of total pressure, as in Fig. 1, points obtained from the unconstrained

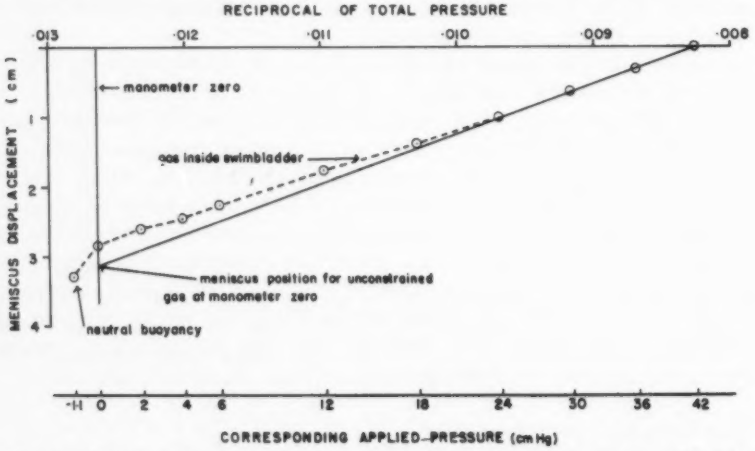

FIG. 1. Meniscus displacement against reciprocal of total pressure in cm Hg for a 16.8-g pollock. Each centimetre displacement indicates an increase of .07378 ml in swimbladder volume.

gas will fall on a straight line and other points on a curve. For the pollock compression of a fish dissected to expose the swimbladder had shown that the swimbladder crumpled inwards at applied pressures above 24 cm Hg suggesting that the swimbladder walls did not compress the gas at applied pressures above this value. This is confirmed by the graph as points for applied pressures of 24 cm Hg and above fall on a straight line. This straight line can be extended to cut the vertical axis representing 0 applied pressure. The volume (Δv) represented by the distance of this intercept from the horizontal axis is the change in volume which the swimbladder gas would have shown if it had not been compressed by the swimbladder walls between 0 and 42 cm Hg applied pressure. Using the formula $V = \frac{(P + \Delta p)\Delta v}{\Delta p}$ where P is the total pressure at 0 applied pressure and Δp the increase in pressure of 42 cm Hg the volume of the unconstrained gas (V) at 0 applied pressure can be found. The true swimbladder volume at test depth can be found by subtracting from this volume (V) the volume represented by the difference in the intercepts of the straight line and the curve at 0 cm Hg applied pressure.

At neutral buoyancy the density of the fish equals that of the sea water. Since the seawater density and the fish mass are known the fish volume at neutral buoyancy can be calculated. At 0 applied pressure the mass of the fish is the same but its volume is smaller by an amount represented by the change in meniscus position between 0 applied pressure and the pressure at neutral buoyancy. From its mass and new volume the density of the fish at 0 applied pressure can be calculated directly.

In the pollock used as an example it was found that the swimbladder of the living fish at a depth of 36 cm of water had a volume of 0.64 ml which was 4.1% of its volume. The density of the fish was 1.027 g/ml giving a sinking factor of 1002.1.

DISCUSSION

The method seeks to measure swimbladder volumes of physoclists by subjecting them to increases in pressure sufficient to remove all constraint by the swimbladder or body walls on the swimbladder gas. An increase in pressure usually initiates gas secretion and during the 6 min required for the series of readings from 0 to 42 and back to 0 cm Hg applied pressure a physoclist capable of rapid gas secretion such as the scup, *Stenotomus versicolar*, studied by Wittenberg (1958) might be able to increase its swimbladder volume by about 1%. However, any increase in volume occurring during the determination would be corrected for as part of the temperature correction, in which any difference in meniscus position after return to manometer zero from the initial reading at zero is distributed equally among the readings.

The method has the advantage of measuring volumes of closed swimbladders quickly while these are still enclosed in the living fish and as the fish is not killed it may be used for further experiments.

ACKNOWLEDGMENTS

The author wishes to thank Dr J. L. Hart whose kindness in providing me with facilities of the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B., made this study possible. Financial support by a Fisheries Research Board of Canada Studentship is gratefully acknowledged.

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NOTES

Widow Rockfish, *Sebastodes entomelas*, New to British Columbia Waters

In British Columbia waters, the rockfish family Scorpaenidae is one of the richest in species. Twenty-seven species were known in British Columbia and the present account adds a 28th (Sunde and Lindsey, 1958; Clemens and Wilby, 1961; Westrheim, 1964, 1965).

A specimen of the widow rockfish, *Sebastodes entomelas* (Jordan and Gilbert, 1880) was kindly forwarded to the senior author by Mr Melvin Stauffer of Alert Bay (Fig. 1). It had been caught on hook and line in Rivers Inlet on the central British Columbia coast. Year of catch was 1964, but date is unknown. The specimen is now in the collection of the National Museum of Canada, Ottawa, Ontario (Cat. No. NMC64-809).

FIG. 1. The widow rockfish, *Sebastodes entomelas*.

A second specimen, collected by the junior author, was caught in a 70-ft Gulf of Mexico shrimp trawl on March 9, 1964, in Quatsino Sound (50°29.4′N lat; 127°45.3′W long) on the west coast of Vancouver Island. This specimen is now in the collection of the Institute of Fisheries, University of British Columbia (Cat. No. BC64-299). Subsequently, during the summer and fall of 1964, 27 additional specimens were collected, for morphometric and meristic data, from commercial and research-vessel catches off the west coast of Vancouver Island and in Queen Charlotte Sound.

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Printed in Canada.

Phillips (1957) reports the geographical range of the widow rockfish as La Jolla, California, to southeastern Alaska. Hitz *et al.* (1961) reported catches off Cape Scott (northwest Vancouver Island). However, Clemens and Wilby (1961) do not record it for British Columbia waters.

The specimens agree closely with the description of those in California (Phillips, 1957). However, the interorbital width is narrower, 3.5–4.1 into head length (3.3–3.9 in California), and the number of pored lateral line scales higher, 52–58 (52–54 in California). In view of the geographical separation of the specimens, these differences do not warrant stress.

The only rockfish species in British Columbia waters with which *S. entomelas* might readily be confused is *S. mystinus*. However, Phillips (1957) reports *mystinus* is noticeably deeper, 2.7–2.9 times in standard length (as opposed to 3.1–3.2), has a deeper caudal peduncle, 8.9–9.6 in standard length (as opposed to 10.5–11.9), and the longest anal ray is longer, 5.8–6.4 in standard length (as opposed to 6.8–7.4). *Sebastodes mystinus* lacks the blotched white bar that runs through the anal fin parallel with the distal edge in *S. entomelas*, and has 50–56 rows of scales below the lateral line instead of 60–66.

The following detailed description of *Sebastodes entomelas* follows the pattern in Clemens and Wilby (1961). The proportions and counts of the 29 British Columbia specimens (169–510 mm FL) are followed, in parentheses, by those of California specimens from Phillips (1957).

Widow rockfish, *Sebastodes entomelas* (Jordan and Gilbert), 1880

Body elongate, deep, depth 2.7–3.3 (3.1–3.2) in standard length. Dorsal and ventral profiles evenly curved. Head relatively short, upper profile almost straight, 3.0–3.2 (3.0–3.1) in standard length; mouth terminal, large, jaws even or lower slightly projecting, upper jaw ending just before midorbit; symphyseal knob absent; eye diameter 3.5–4.5 (3.8–4.5) in length of head; interorbital space at midorbits slightly convex, broad, 3.5–4.1 (3.3–3.9) in head length; cranial spines: nasal; and weak prefrontal (in adults); cleithral, broad; supracleithral; opercular 2, moderate; preopercular medium, simple; lacrymal lobes and spines, absent; rakers on first gill arch 32–36 (35–37). Fins: dorsal (1), XIII, 14–16 (XIII, (14)15–16), moderately notched, membranes of spinous portion slightly incised, low, shorter than longest rays; anal, III, 8–10 (III, 8); pelvic, I, 5 (I, 5), thoracic, not reaching anus, pectoral 17–18 (17–19), 9–10 (8–10) unbranched, short, not reaching anus. Scales: ctenoid; in oblique rows below lateral line,[1] 58–66 (60–66). Pores: on lateral line 52–58 (52–54). Colour: Grayish-black to brown on dorsal surface; paler below; fairly uniform, but some mottlings on back; a dark spot on operculum and one on subopercular; a dark suborbital streak extending down and back from midorbit; fins dusky; anal with blotched white bar paralleling distal edge; peritoneum black or silver-grey with black dots. California specimens reported as uniformly dusky-brown, with traces of light yellow; fins dusky, tinged with brown except for caudal; specimens under 10 inches with vague streaks of orange (Phillips, 1957). Length to 20½ inches.

Distinguished by the slightly convex interorbital space without spines, the small prefrontal spines, the lower jaw projecting only slightly, the dark peritoneum, the blotchy white bar on the anal fin, and 58–66 diagonal scale rows below the lateral line.

[1]Phillips' (1957) count of scales below the lateral line appears more diagnostic than the count of those above the lateral line used by Clemens and Wilby (1961).

Range is from La Jolla, California, to southeastern Alaska.

The widow rockfish is a minor component in the rockfish landings of the British Columbia trawl fleet.

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Received for publication May 25, 1965.

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Relative Rates of Degradation of Some Organisms Consumed by Marine Salmon

In the course of interpreting data concerning stomach contents of salmon (*Oncorhynchus* sp.) captured on the high seas it was apparent that it would be desirable to have an appreciation of the relative rates of degradation of

TABLE I. Degradation of some marine organisms in swine pepsin.

Organisms	Colour and weight in intact condition	Condition after degradation			
		1 hr	2 hr	3 hr	4½ hr
Copepods	Red Samples 3 g 14 g	Largely intact, red.	Largely in fragments, still identifiable to species.	Little change.	Few pieces of exoskeleton, unidentifiable to species.
Euphausiids	Whitish Samples 4 g 6 g 12 g	Small samples in fragments, eyes conspicuous. Large sample intact.	Small samples reduced to exoskeleton and eyes. Large sample with fragments.	Pieces of exoskeleton and eyes only, color pink. Large sample, with some intact specimens.	No change. Large sample still with some intact specimens, eyes conspicuous.
Squid	Grey Samples 4 g 47 g	Small sample, few fragments. Large sample, skin gone.	Small sample pink, miscellaneous fragments. Large sample head and mantle in pieces.	Large sample pink, pieces of hook, beak, pen and mantle remaining.	Not identifiable.
Fish	Black Samples 2 g 4 g	Largely liquid, few fragments of body, eyes, and vertebrae.	Few fragments of muscle and vertebrae.	Black liquid, few traces of vertebrae.	All material in solution.
Mixed zooplankton	Brown 9 g	Some broken specimens.	Traces of copepods, euphausiids in pieces.	Little change.	Traces of exoskeleton.
Zooplankton, fish, and, squid	Red, black, grey 27 g	Fish in fragments, others mostly intact.	Copepods and fish in fragments.	Fish, liquid. Mantle, and pen only of squid. Copepods in pieces, euphausiid exoskeletons intact.	Small pieces of squid mantle and some intact euphausiid exoskeletons remaining.

J. FISH. RES. BD. CANADA, **22**(6), 1965.
Printed in Canada.

typical food items. Pepsin from salmon stomachs would be the most suitable proteolytic agent, but is not commercially available, and according to Norris and Elam (1940) it is difficult to collect. Accordingly, tests were conducted using swine pepsin, which though different in many respects from fish pepsin (Norris and Elam, 1940; Norris and Mathies, 1953; Fruton and Bergmann, 1940; Ishihara, 1960) may nevertheless indicate some of the relative degradation rates which occur in fish stomachs.

The organisms, which were known to be species eaten by salmon, were collected and frozen at sea. Thawed, drained samples of undamaged specimens were weighed and placed in conical flasks with a pepsin–hydrochloric acid solution of pH 1.8 (0.2 g triple crystallized swine pepsin per 1000 ml 1.5% hydrochloric acid) at a ratio of 10 ml/g. The flasks were placed in a shaker bath at 37 C and were examined at intervals.

Regardless of whether the organisms were treated separately or were grouped together it was clear that the rate of degradation was in the order (1) fish (salmonids, myctophids, and hexagrammids); (2) squid (gonatids); (3) copepods; (4) euphausiids (Table I). Within an hour, digestion of fish was advanced, and by 3 hr only a few traces of vertebrae had not been rendered into a black liquid. The same was true of fresh as of frozen specimens. Similarly, squid were largely digested, except for hard parts such as the beak, within 3 hr. By contrast the crustacea, presumably by virtue of their exoskeletons, were resistant to degradation, and could still be identified (particularly the euphausiids) after 4½ hr.

The rates of digestion indicated by these tests are not of course representative of natural digestion of salmon stomach contents, which takes place at 5–10 C, at a pH of 1.8–3.0 and with the continuous addition of salmon pepsin and other enzymes. They nevertheless serve to indicate differences in rates of degradation that would suggest the need for caution in inferring food habits from stomach contents.

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Received for publication June 17, 1965.

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New Size Record for Greysole (*Glyptocephalus cynoglossus*)

Although a number of authors cite size records for flatfish such as American plaice, *Hippoglossoides platessoides* (F.), and halibut, *Hippoglossus hippoglossus* (L.), there appears to be no maximum size recorded for greysole, *Glyptocephalus cynoglossus* (L.). The species is a common deep-water pleuronectid found in subarctic waters. Bigelow and Schroeder (1953) suggest that greysole seldom exceed 25 inches (63 cm) in length and 4 lb (1820 g) in weight. Perlmutter (1961) mentions 2 ft (61 cm) and 4 lb as a maximum size. For European waters, Jenkins (1950) states that records above 19 inches (48 cm) are very rare, but gives no weight.

On May 28, 1965, a greysole (Fig. 1) over 31 inches (78 cm) total length and 11 lb (5000 g) in weight was captured off Cape Breton Island by Danish seiner captain Victor Sangster. To my knowledge, this is the largest greysole recorded from either Canadian or European waters. Details of dimensions and meristic characters are shown in Table I.

The sex and stage of maturity were most unusual. The fish was either an undeveloped male, or one in which the testis had atrophied. Only the left testis was present. There was no sign of a gonad on the right side, but a long section of looped intestine extended posteriorly into the body (Fig. 2) (presenting the illusion of an ovary). More than 3000 greysole have been examined by the author yet no anomaly of this type had been observed before.

TABLE I. Capture details and body measurements of a large greysole taken off Cape Breton Island.

Date:	May 28, 1965	Depth: 92 fath (168 m)	
Location:	47°09′N; 60°31′W	Vessel:	*Bonnie Lou II*
Measurements		*No. fin rays*	
Weight:	11 lb (4983 g)		
Total length:	781+ mm	Dorsal:	109
Body width:	320 mm	Anal:	94
Orbit (horizontal diam.):	33 mm	Pectoral:	11
Head length:	132 mm	Pelvic:	6
Pectoral fin length:	70 mm		
Pelvic fin length:	42 mm		
Maxillary length:	44 mm		

J. FISH. RES. BD. CANADA, **22**(6), 1965.
Printed in Canada.

The age of the fish was estimated from the otoliths. The first 18 annuli were well spaced and clear, but subsequent rings were difficult to interpret. The total age was estimated at between 36 and 38 years, whereas previously the oldest greysole observed in Cape Breton waters was 28 years of age.

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Received for publication July 12, 1965.

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(Fig. 1 and 2 *opposite*)

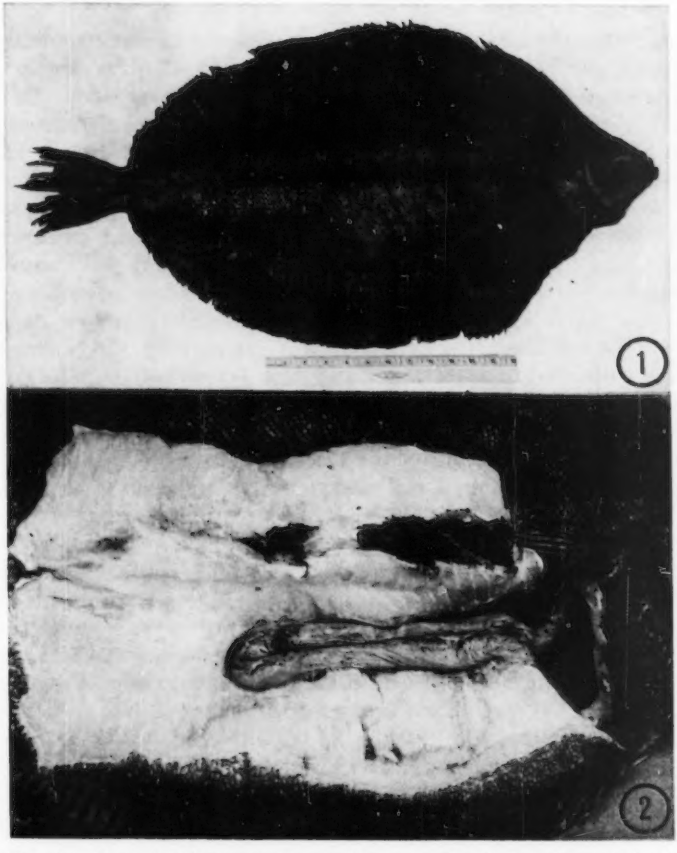

FIG. 1. Greysole, *Glyptocephalus cynoglossus*, caught off Cape Breton Island, May 28, 1965.

FIG. 2. A long section of looped intestine giving an illusion of an ovary.

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Precocious Sexual Development in Male Post-Smolt Atlantic Salmon Reared in the Laboratory

Precocious sexual development of male parr or even underyearling Atlantic salmon, *Salmo salar* Linnaeus, is common in nature (White, 1934; Jones, 1959). This report concerns sexual development at the post-smolt stage. The term post-smolt is used here to describe the life stage of the salmon during the period between the smolt and grilse stages. Grilse are defined as fish which mature and return to fresh water after 1 year in the sea. Some males in the laboratory became sexually mature after only 4–7 months of post-smolt growth. These were being used for studies of growth in water of various salinities.

In June 1964, groups of 90 one-year-old hatchery-reared smolts were put into 6-ft diameter cylindrical fiberglass tanks in which the salinities were maintained within ±1.5‰ of the following levels: 7, 15, 21, and 30‰. A control group was kept in fresh water. Temperature followed the natural seasonal variation (between 4 and 16 C) and at any given time was nearly identical among the five tanks. The fish were fed a mixture of ground fresh beef liver (45%), Atlantic herring (45%), and Purina trout chow (10%). The diet was supplemented with fresh euphausiids. Fish were fed to satiety three times daily during the summer and less frequently as the temperature fell.

Twelve mature or maturing males were found among approximately 400 surviving post-smolts 4–7 months after the experiment was started (Table I). The sex ratio in the group of 400 fish is not known and it is therefore not possible to say what percentage of males matured. However, of 66 fish which died, 28 were males and 38 were females. Figure 1 shows the extent of gonad development in one of the fish examined. Six of the first seven individuals listed had died and their mature condition was discovered during dissection. On December 22 the individual in 7‰ salinity was examined because it had spawning colors like those seen in nature. The remaining five ripe fish were discovered on January 26 when all fish were examined for maturity by gently pressing their sides.

None of the sexually mature fish had a hook which develops on the tip of the lower jaw of large, mature, male Atlantic salmon. The mature individual examined on December 22 and the three found in 21‰ salinity on January 26 were reddish-brown in color in contrast with the immature fish which were silvery. The two found in 30‰ on January 26 were not distinguishable by color from immature fish. The scales of sexually mature males were much more firmly attached than those on the immature fish. Spawning salmon in nature have firmly attached scales (Jones, 1959).

In nature it is unusual to find a mature Atlantic salmon which has returned to fresh water later in the same year in which it went to sea as a smolt. Six

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TABLE I. Data concerning sexually mature male post-smolts reared in the laboratory.

Date observed	Length	Weight	Gonad weight	Salinity
	cm	*g*	*g*	‰
Oct. 7, 1964	26.6	231	–	21
Oct. 10, 1964	33.5	435	1.6[a]	7
Oct. 16, 1964[b]	28.1	268	14.4	15
Dec. 22, 1964	35.4	473	–	7
Jan. 4, 1965	30.5	311	–	21 or 30
Jan. 9, 1965	32.0	352	8.0	fresh water
Jan. 24, 1965	28.5	251	10.0	30
Jan. 26, 1965	29.3	283	–	21
Jan. 26, 1965	33.6	422	–	21
Jan. 26, 1965	33.8	429	–	21
Jan. 26, 1965	30.6	316	–	30
Jan. 26, 1965	38.9	702	–	30

[a]The gonad weights of immature males were less than 0.3 g.
[b]This fish shown in Fig. 1.

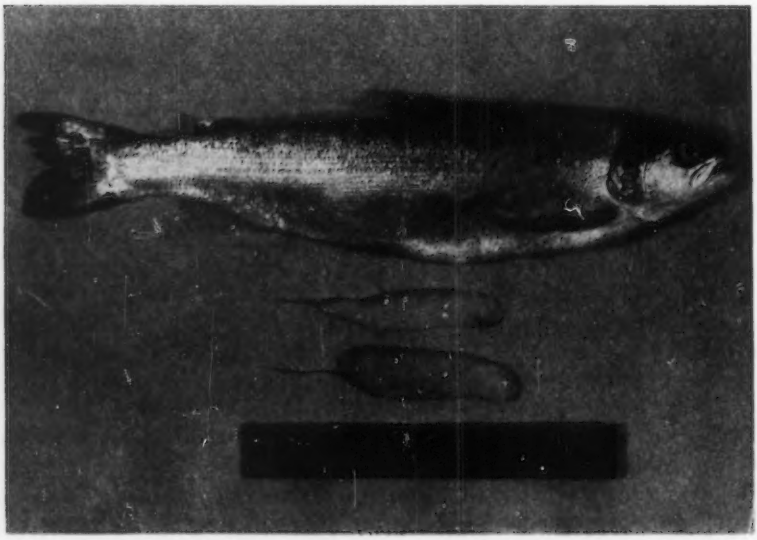

FIG. 1. Sexually mature post-smolt reared in 15‰ salinity. Testes have been removed from body cavity to show extent of their development.

captures of such post-smolts or pre-grilse have been reported in the British Isles by Menzies (1914), Hutton (1950), and Shearer (1963). These fish were conspicuously smaller than grilse and some had been incorrectly identified as sea trout, *Salmo trutta* Linnaeus, by anglers. Murray (FRB, 1960, p. 53; 1961, p. 44; 1962, p. 49) observed three post-smolts in 1959 and one each year in 1960 and 1961 among the ascending adults passing upstream through a counting fence in the estuary of the Little Codroy River in southwestern Newfoundland. No such post-smolts have been observed at a counting fence, 7 miles above tidehead on the Northwest Miramichi River, New Brunswick, where nearly 48,000 ascending adults were counted between 1950 and 1963 (Henderson *et al.*, MS, 1965). From 1952 to 1964, Elson (personal communication) examined over 1000 post-smolts taken in herring weirs along the upper Bay of Fundy coast of Nova Scotia. All had very loose scales characteristic of sexually immature salmon. In no case were gonads conspicuously developed.

It may be significant that the laboratory fish described in this report became smolts as 1-year-olds. Most Canadian salmon hatched and grown in nature would not have advanced beyond the parr stage in 1 year. As far as known, few salmon from rivers in eastern Canada smoltify at age 1, most usually doing so at age 2 and upwards. The accelerated development through the parr and smolt stages in salmon reared under laboratory conditions may have been responsible for the attainment of sexual maturity in post-smolts, a life stage in which sexual maturity has rarely been observed. There may be, therefore, a question of the efficacy of producing smolts in the hatchery in 1 rather than 2 years if significant numbers of yearling smolts give rise to small adults. It remains to be seen whether or not hatchery-reared yearling smolts give rise to precocious males when released in nature as they did in the laboratory.

Evropeytseva (1960) deduced that male Baltic salmon parr which have reached a body size as great as that of smolts but which do not smoltify are probably in the process of precocious sexual development — a process which she asserts is incompatible with smoltification because the two are "biologically opposite processes." She reports that most large parr which did not smoltify were in fact maturing males. In a later work, Evropeytseva (1962) found that three different ecological forms of Atlantic salmon (landlocked from Lake Ladoga, Baltic, and sea-run salmon from Kola Peninsula) when held in fresh water beyond the time of smolt migration reverted to the parr phase at different rates and that such reversion was reflected in different respiratory and growth rates and different times to death in highly saline (56‰) water. In the present study the fish withstood the salinities imposed and grew rapidly during the summer, many reaching lengths of 30 cm and weights of 350 g by October. They seemed to be smolts both functionally and by appearance yet some of the males developed sexual maturity.

Two sexually mature, milting, male smolts were found in the seaward smolt run during May–June 1964 in the Northwest Miramichi River. Power (1959) found sexually mature male smolts in rivers flowing into Ungava Bay,

Labrador. Saunders (1960) reports that of 43 milting male parr which were marked as they moved into the estuary of Ellerslie Brook, Prince Edward Island, nine were recaptured as smolts in the estuary the next spring. Jones (1959) examined a large sample of smolts from various British rivers and found that 60% of the males were spent. The possible relationship between smoltification and precocious sexual development of males is not clearly understood. Further study of this relationship might help answer the important question "Why do some Atlantic salmon mature as grilse while others do not mature until after having spent 2 or 3 years in the sea?"

We are grateful to Miss Judith Sydor and Mr Harry Sampson who helped in rearing the fish. Drs M. W. Smith and P. F. Elson offered helpful suggestions for the execution of the project and interpretation of results. Drs J. C. Medcof and D. W. McLeese gave helpful suggestions for the manuscript. Salmon were provided by various hatcheries through the Fish Culture Development Branch of the Department of Fisheries of Canada.

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Received for publication May 7, 1965.

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The Fall Domestic Fishery at Snowdrift, Northwest Territories

In addition to being utilized for commercial and angling purposes, fish from Great Slave Lake provide food for some residents and their dogs. The magnitude of this domestic fishery was estimated in 1945 at 1,000,000 lb annually (Rawson, 1947). Because of an increased interest in this fishery, the results of a more recent survey at one place are presented.[1]

Snowdrift, an isolated Indian community (VanStone, 1963) in the East Arm of Great Slave Lake, had a population of 163 residents who owned 173 dogs. The survey consisted of inspection of domestic fishing (Fig. 1), weighing fish, and soliciting information from the residents. Field work was carried out between October 4 and November 16, 1961.

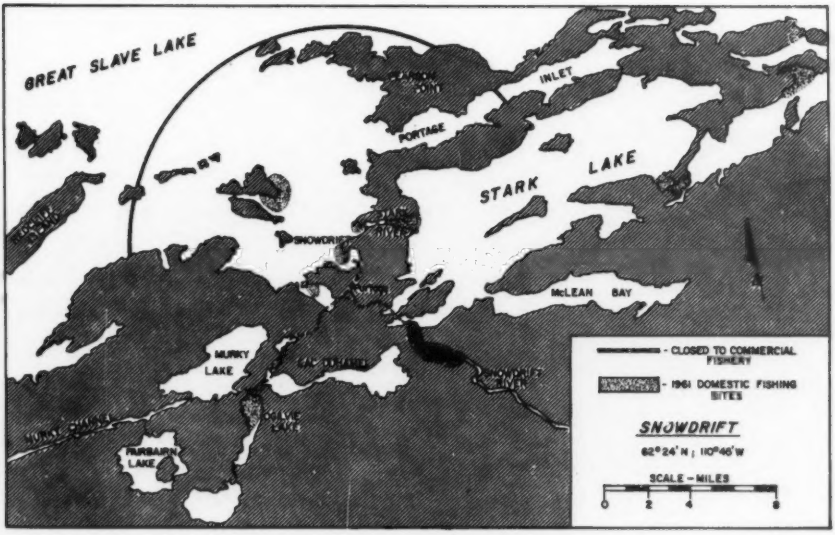

FIG. 1. Locations of fall domestic fishing at Snowdrift, Northwest Territories, in 1961.

The fishermen used nylon and cotton gill nets of variable length and three different mesh sizes. Instead of conventional leads and floats, most nets were equipped with rocks and sticks which became snarled in the webbing and hindered fishing.

Interviews on the catch from 5785 yards of net revealed that 2908 fish, equivalent to 10,417 lb, were taken. The overall catch per net expressed in

[1]Details are available in a mimeographed manuscript report (No. 738) which is available at all stations of the Fisheries Research Board of Canada.

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Printed in Canada.

TABLE I. Average pounds per 100-yd net and estimated total catch and effort at Snowdrift fall domestic fishery, 1961.

Item	Locations					
	Snowdrift River	Stark River	Stark Lake	Ogilvie Lake	Great Slave Lake	All
Yardage examined	1,430	1,225	1,050	680	1,400	5,785
Pounds per net						
Lake whitefish, *Coregonus clupeaformis*	245	43	63	140	86	118
Lake trout, *Cristivomer namaycush*	t[d]	72	63	0	27	33
Others[a]	39	39	15	10	27	29
Total:	284	154	141	150	140	180
Catch						
Lake whitefish	16,647	836	1,871	6,756	2,038	28,148
Lake trout	0	1,291	2,530	0	2,354	6,175
Others[a]	2,857	694	986	888	3,656	9,081
Total:	19,504	2,821	5,387	7,644	8,048	43,404
No. of Nets	68[b]	18[c]	35[c]	48[b]	24[b]	193

[a]*Esox lucius, Catostomus catostomus, Leucichthys* spp., *Lota lota, Thymallus arcticus, Prosopium cylindraceum.*
[b]Based on lake whitefish.
[c]Based on average of lake whitefish and lake trout.
[d]t = less than 1 lb.

terms of a 100-yard net was 180 lb with lake whitefish, *Coregonus clupeaformis*, contributing two-thirds or 118 lb (Table I). The Snowdrift River catch per net was nearly double that found at each of the other four locations, which were similar.

The estimated catch during the fall domestic fishery, derived from inquiry and inspection, was 43,400 lb, consisting of 65% lake whitefish, 14% lake trout, *Cristivomer namaycush*, and 21% of six other species (Table I). Nearly half of the catch came from the Snowdrift River. Less than 20% came from Great Slave Lake, even though the region within 10 statute miles from Snowdrift (Fig. 1) originally was reserved exclusively for this domestic fishery (Anon., 1949). The estimated number of nets, derived from interviews for 24% of the estimated catch, was 193.

The survey indicated that, while the potential fish consumption of the Snowdrift community was not met by the fall domestic fishery, it is apparent that any lack was not due to a scarcity of fish in the five fishing locations.

Mr Arne Steinwand, then Hudson's Bay Company manager at Snowdrift, rendered assistance in numerous ways.

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Received for publication July 20, 1965.

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Phytoplankton Pigment Nomographs

The amount of chlorophyll *a*, *b*, and *c* in plankton populations is generally estimated by spectrophotometric analysis of acetone extracts of the plankton. The estimation is carried out by measuring the optical density of the acetone extract at 665, 645, and 630 mμ. These values are corrected for any absorption at 750 mμ and the quantity of pigments is determined from three simultaneous equations. When large numbers of samples are involved, considerable time can be saved by converting the simultaneous equations into a nomographic form (Duxbury and Yentsch, 1956). The nomographs constructed here are for use with the revised equations for ascertaining chlorophylls as discussed by Parsons and Strickland (1963).

The following description for the use of the nomographs is given for chlorophyll *a*. (By using the appropriate nomographs, the estimation of chlorophylls *b* and *c* follow a similar procedure.) Corrected optical densities at 645 and 630 mμ (D_{645} and D_{630}) are plotted on their respective lines and joined with a straight edge. The intercept on line Q is then lined up with the corrected optical density at 665 mμ (D_{665}). The intercept on the C*a* line then gives the concentration of pigment. The actual units of concentration will be the same as are employed in the equation shown in Parsons and Strickland (1963) or in "A Manual of Sea Water Analysis" by J. D. H. Strickland and T. R. Parsons (Bulletin No. 125, 2nd edition (Revised), Fish. Res. Bd. Canada, 1965).

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Received for publication October 25, 1965.

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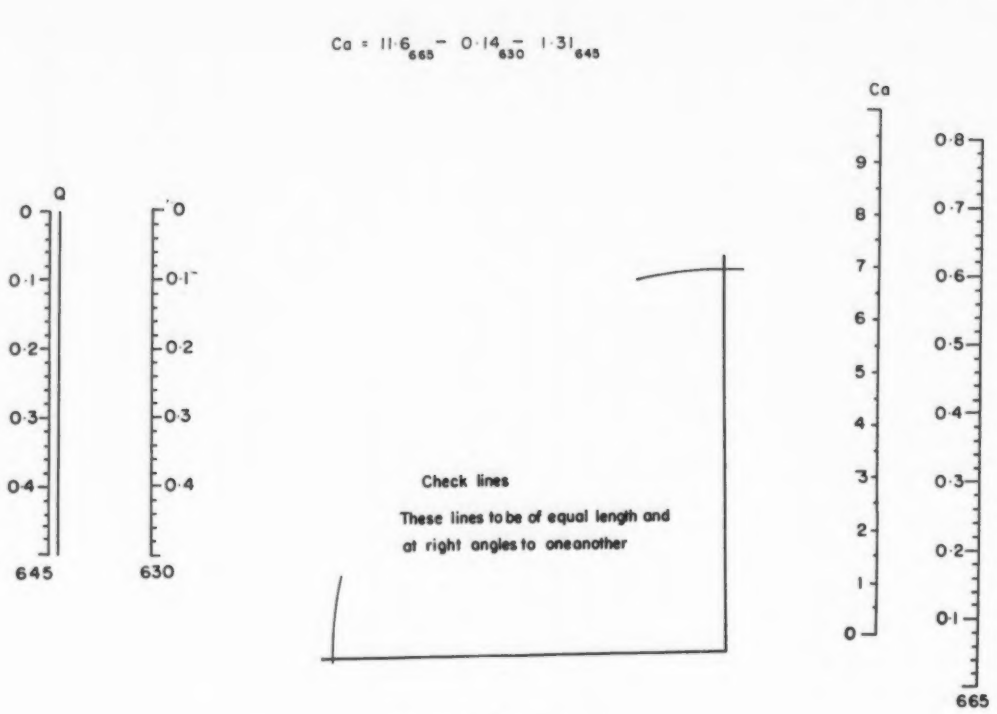
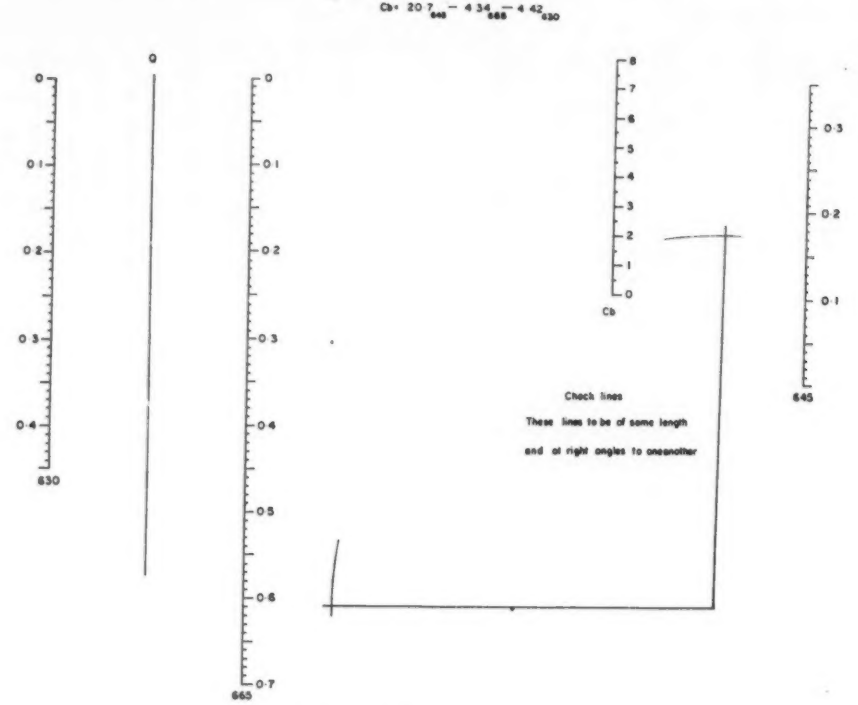
(Note: *Nomographs on following pages.*)

J. Fish. Res. Bd. Canada, **22**(6), 1965.
Printed in Canada.



Chlorophyll *a* nomograph.

Stephens — J. Fish. Res. Bd. Canada



Chlorophyll *b* nomograph.

Chlorophyll *c* nomograph.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

956. **Tibbo, S. N., L. M. Lauzier, and A. C. Kohler.** 1965. Canadian fisheries research extends to Caribbean Sea. Trade News, **17**(11, 12): 3–9.

957. **Nota, D. J. G., and D. H. Loring.** 1964. Recent depositional conditions in the St. Lawrence River and Gulf — a reconnaissance survey. Marine Geol., **2**: 198–235.

958. **Idler, D. R., and H. C. Freeman.** 1965. A demonstration of an impaired hormone metabolism in moribund Atlantic cod (*Gadus morhua* L.). Canadian J. Biochem., **43**: 620–623.

959. **Werner, A. E.** 1965. Suspended solids from mill effluents. Canadian Pulp and Paper Industry (April), p. 109–114.

960. **Sprague, John B.** 1965. Apparatus used for studying avoidance of pollutants by young Atlantic salmon. Biological Problems in Water Pollution. Third Seminar. 1962. Robt. A. Taft Sanitary Engineering Center, United States Public Health Service, Publ. No. 999-WP-25, p. 315.

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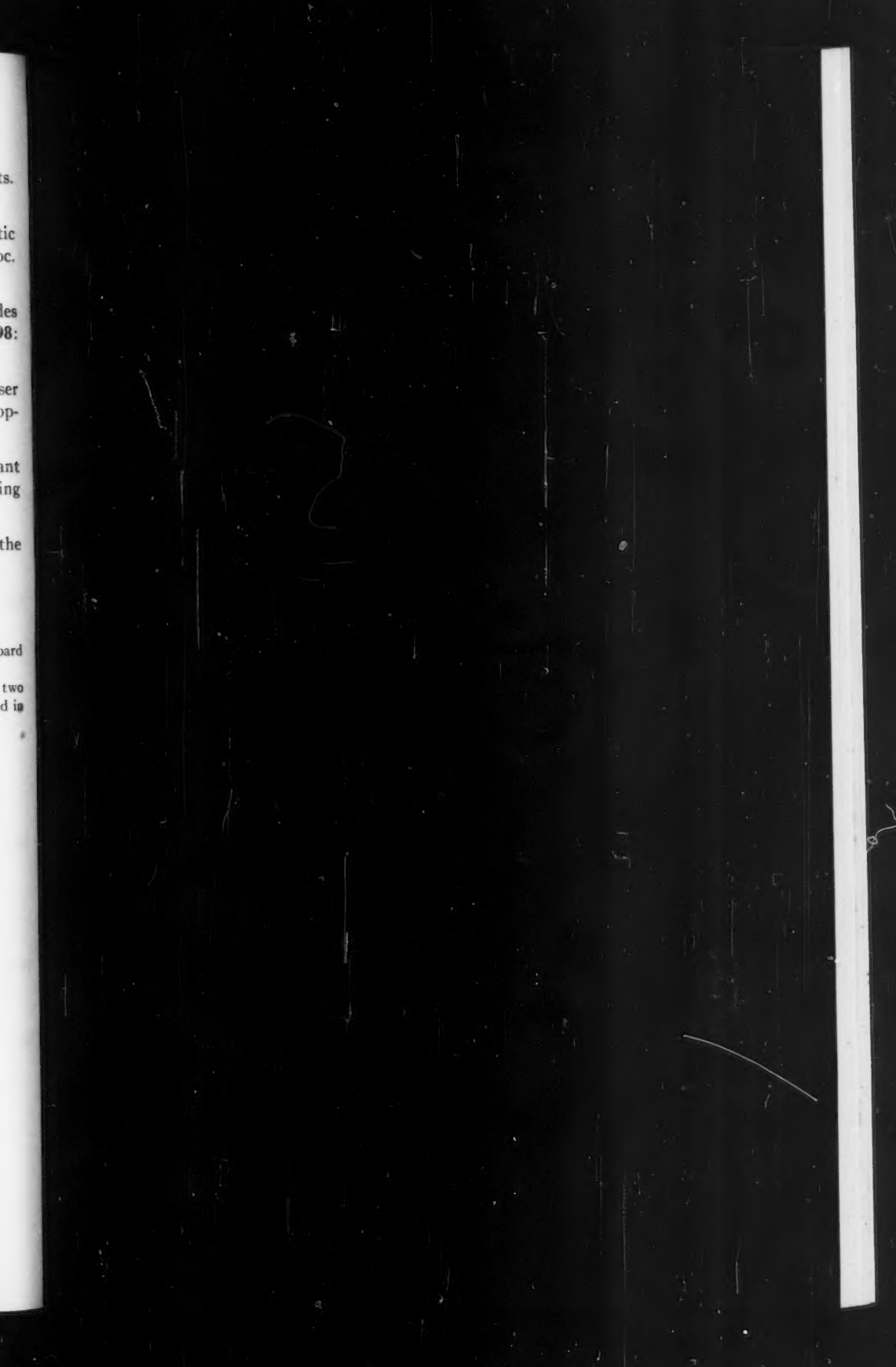
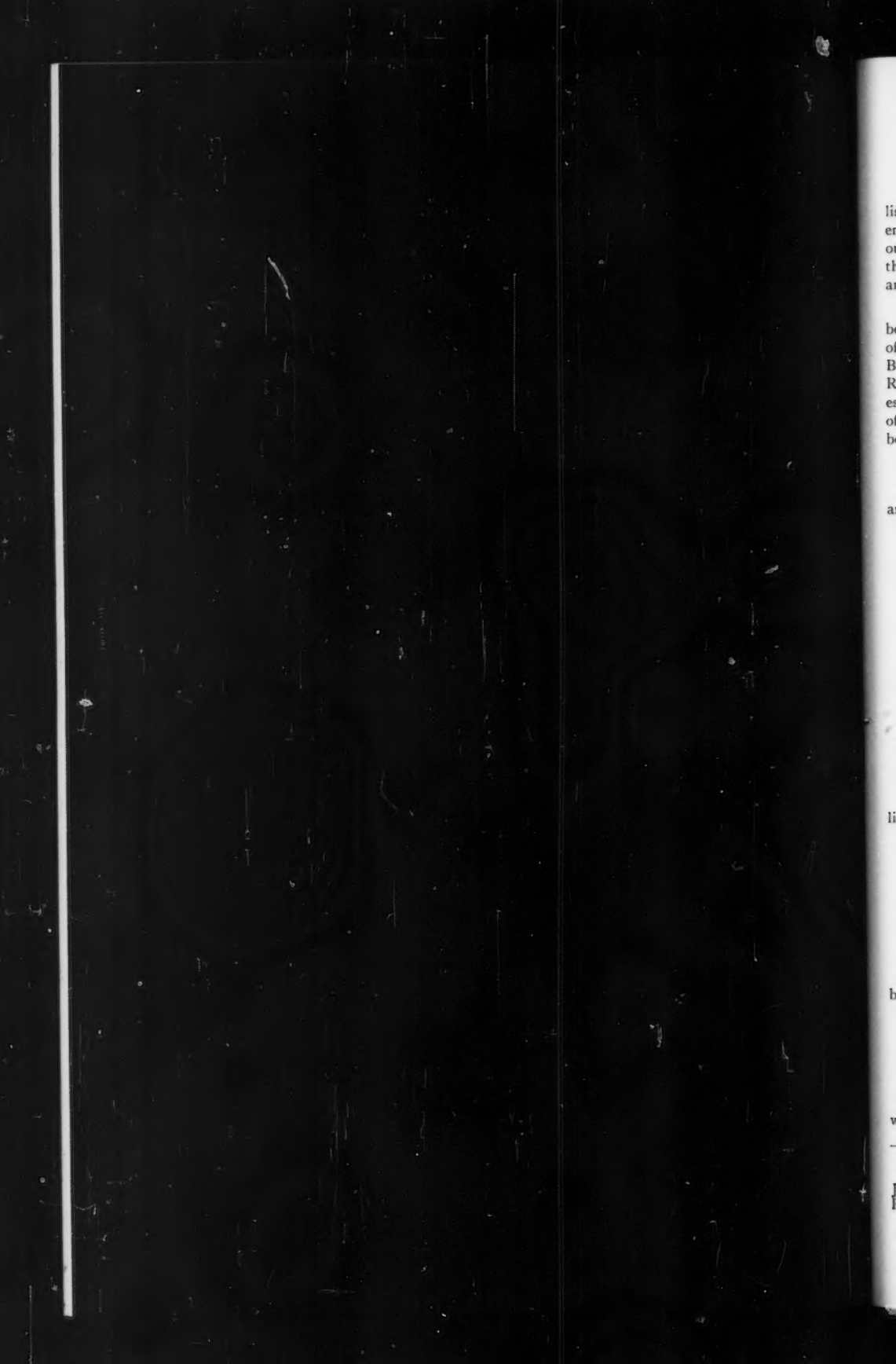
969. **Tarr, H. L. A., and F. Claggett.** 1965. The effect of antioxidant treatment on the metabolizable energy and protein value of herring meal. Poultry Science, **44**(3): 679–685.

970. **May, A. W.** 1965. New cod fishing grounds off Labrador and the northeast coast of Newfoundland. Trade News, **16**(12): 3–6.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies," composed of two parts. These are distributed to a selected mailing list. (Articles numbered 861–885 appeared in the Studies for 1964, Part 1.)





INDEX TO PUBLICATIONS FOR 1965[1]

In 1957 the Fisheries Research Board of Canada published Bulletin No. 110 containing a list of the articles in most of its series of publications and Studies that had appeared up to the end of 1954, together with a subject–author index to many of those series. That Bulletin is now out of print. A successor to it that will list and index *all* Board publications and Studies up to the end of 1964, plus many items that did not get included in the Studies, is nearing completion and is expected to appear in 1966.

From 1955 to 1964 inclusive, a subject–author index to all articles in the Journal only has been included in the last issue (No. 6) of each Journal volume. Commencing with this 1965 volume of the Journal, the index is based on: (a) Volume 22 of the Journal of the Fisheries Research Board of Canada; (b) No. 125 (second edition, revised) and 149 of the Bulletins of the Fisheries Research Board of Canada; (c) Circular series from the Fisheries Research Board of Canada establishments issued in 1965 (appearing in time to be included); and (d) Studies (No. 886–970) of the Fisheries Research Board of Canada (reprints of articles published in other periodicals, bound annually in two parts). Lists of titles of individual articles immediately follow the index.

The expansion of the indexing necessitates the following explanatory notes:

Abbreviations for types of publications — The types of publications for which lists of articles are given are abbreviated thus:

J — Journal of the Fisheries Research Board of Canada
B — Bulletin of the Fisheries Research Board of Canada

Circulars of the Fisheries Research Board of Canada:

CAG — Arctic Biological Station, Ste. Anne de Bellevue, Que.
CHN — Halifax Laboratory, Halifax, N. S.
CLG — Biological Station, London, Ont.
CNG — Biological Station, Nanaimo, B. C. (General series)
CNS — Biological Station, Nanaimo, B.C. (Statistical series)
CJG — Biological Station, St. John's, Nfld.
CPO — Pacific Oceanographic Group, Nanaimo, B.C.
CSG — Biological Station, St. Andrews, N.B. (General series)
CSS — Biological Station, St. Andrews, N.B. (Statistical series)
CVG — Vancouver Laboratory, Vancouver, B.C.
S — Studies of the Fisheries Research Board of Canada

Other abbreviations — B 125R refers to the 1965 revised edition of Bulletin No. 125 published under the same title in 1960.

The Provinces and Territories of Canada are abbreviated to:

Alta. (Alberta)	N.W.T. (Northwest Territories)
B.C. (British Columbia)	Ont. (Ontario)
Man. (Manitoba)	P.E.I. (Prince Edward Island)
N.B. (New Brunswick)	Que. (Quebec)
Nfld. (Newfoundland)	Sask. (Saskatchewan)
N.S. (Nova Scotia)	Yuk. (Yukon)

Certain geographical areas (particularly oceans) have their major subdivisions designated by N. (north), S. (south), E. (east), W. (west), NE. (northeast), etc.

Certain international commissions are commonly referred to as:

ICNAF (International Commission for the Northwest Atlantic Fisheries)
INPFC (International North Pacific Fisheries Commission)
IPSFC (International Pacific Salmon Fisheries Commission)

In the index references, "re" is frequently used to imply "in relation to," "in connection with," and similar meanings; "vs." to imply such meanings as "in contrast to," "as opposed to."

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[1]Prepared by Neal M. Carter.

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A

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940 (southern N.S. haddock)
952 (Fraser River odd-year pink salmon run)

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J 22(6): 1455 (thermal, of goldfish)

Achromobacter cholinophagum
S 933, 936 (new species that ferments choline)

Acid (*see* Acids; *also* under names of individual acids)

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B 125R: 83 (determination for sea water)
S 929 (lysine in fish protein concentrates)

Acids, fatty (*see also* Lipids)
J 22(1): 131 (of squid lipids)
(5): 1107 (of various marine lipids)
S 921 (and esters: flame ionization detector re carbonyl carbon)
932 (of blubber from lactating grey seal)
942 (gas chromatography of ester mixtures)
944 (stereospecific distribution in triglycerides)
945 (cod liver oil and leatherback turtle dermal oil)

Acids, nucleic (*see also* Nucleosides)
S 895 (deoxyribonucleic acids of Copepoda)

Acipenser fulvescens (*see* Sturgeon, lake)

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(4): 875 (dimethyl-β-propiothetin)
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932 (grey (Atlantic) seal)
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(6): 1397 (carp muscle effort metabolism)

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(2): 568 (American plaice, from otoliths)
(2): 605 (composition re size of Nfld salmon)
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(6): 1477 (sockeye and chum salmon by scales)
(6): 1565 (new record for witch flounder)
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Alepocephalus tenebrosus (a deep-water fish)
J 22(5): 1151 (description and taxonomy of NE. Pacific)

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Aluminium compounds
S 957 (in St. Lawrence River and Gulf sediments)

Amberjack, greater (*Seriola dumerili*)
S 956 (Canadian research in Caribbean Sea)

Ammodytes (*see* Sandlances)

Ammonia
B 125R: 83 (determination for sea water)

Amphipoda
J 22(4): 1103 (*Anonyx* predation on lobsters)

Analysis
B 125R (manual for sea water)

Anderson, John Murray
J 22(2): 503 (DDT on temperature selection)

Andrews, Cater William
J 22(2): 369 (*Salmo salar* behavior)

Angiography
S 934 (radiography of Pacific salmon cardiovascular system)

Angling
S 920 (forest spraying re Atlantic salmon)

Anomalies (*see also* Abnormalities)
J 22(1): 219 (white sucker fins)

Anonymous
CPO 1965-3 (cruise report, *Ehkoli*)
1965-5 (cruise report, *Ehkoli*)
1965-7 (cruise report, *Whitethroat*)
1965-8 (cruise report, *Whitethroat*)
CJG 12 (Newfoundland fisheries)
S 890 (summaries of ICNAF research, 1962, by subareas)
893 (Atlantic salmon and trout)
905 (Atlantic salmon research)
925 (INPFC Canadian research)
926 (INPFC Canadian research)
965 (Atlantic salmon research)

Anonyx (Amphipoda)
J 22(4): 1103 (parasitism on lobster)

Anoplopoma fimbria (*see* Sablefish)

Antia, Navel Jamshedji
J 22(3): 793 (phytoplankter enzymes)

Antibiotics (other than tetracycline types) (*see also* Preservatives)
J 22(1): 243 (effect on piscine bacteria)
S 889 (for fish preservation)

Antibiotics (tetracycline types)
J 22(1): 117 (in shrimp preservation)
(1): 243 (effect on piscine bacteria)
S 889 (for fish preservation)

Antioxidants (*see also* Rancidity, oxidative)
J 22(1): 53 (salt vs. polyposphate, for frozen fish)
(4): 929 (effects of metal salts on lean cod muscle, and estimation of)
CVG 34 (effect in improving herring meal nutritive value)
35 (for control of herring meal spontaneous heating)
S 969 (effect in improving herring meal nutritive value)

Aplodinotus grunniens (*see* Drum, freshwater)

Apparatus
B 125R: 7 (for sea water analyses)
S 912 (for seawater aquaria system)
960 (for studying pollutant avoidance by young Atlantic salmon)

Applegate, Vernon Calvert
J 22(3): 695 (migrating sea lampreys)

Aquaria
CHN 21 (for holding and displaying live lobsters)
S 912 (seawater system for experimental tanks)
913 (a cause of alkalinity in freshwater supply for)

Arctic Ocean (Canadian) (*see also* Oceanography)
J 22(2): 543 (zooplankton, especially *Calanus* and *Microcalanus*)

Argis dentata (a decapod)
J 22(1): 69 (larvae and megalopa from Ungava Bay)

Atrahantseff, Sergei
J 22(6): 1407 (brittlestar distribution)

Athabaska, Lake
S 900 (availability of fishes)
908 (limnology)

Atheresthes stomias (*see* Flounder, arrowtooth)

Atlantic Ocean, northwestern (*see also* Hydrography; Oceanography)
J 22(1): 1 (new *Calocaris* species)
(2): 433 (harp seal migrations)
(2): 543 (zooplankton)
(2): 621 (Canadian inshore monkfish seasonal distribution)
(4): 977 (list of Mollusca from, 1946–61)
S 938 (sealing industry)

Atlantic Ocean, western (*see also* Hydrography; Oceanography)
J 22(5): 1313 (postlarval stage of sandlances)

Availability
S 900 (of Canadian fishes)

B

Babine Lake system, B.C.
J 22(4): 1025 (tracing sockeye smolt movements by sonar plus photography)

Bacciger (Trematoda)
S 937 (review of genus)

Bacillariophyta (*see also* Diatoms)
J 22(3): 793 (phosphatase activity)
(4): 1083 (carbon balance)
(5): 1107 (lipid fatty acids)

Bacteria (in fish processing)
J 22(3): 755 (*Pseudomonas fragi* for inhibiting flesh browning)
S 889 (control of bacterial spoilage in fish)
933, 936 (new species that ferments choline)

Bacteria (reaction towards inhibitors)
J 22(1): 117 (re antibiotics and Mg ion)
(1): 243 (re tetracycline and chemotherapeutic antibiotics)

Bacteria, disease
J 22(3): 713 (for oral immunization of rainbow trout)

Baker Lake, N.W.T.
J 22(1): 239 (deepwater salinity)

Balanus (*see* Barnacle)

Bankia setacea (a mollusc) (*see* Shipworms)

Barber, Frederick George
J 22(1): 225 (current observations)

Barium compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)

Barnacle
S 895 (*Balanus nubilis* deoxyribonucleic acids)

Barraclough, William Edward
J 22(5): 1305 (dusky sculpin)

Barracuda, great (*Sphyraena barracuda*)
S 956 (Canadian research in Caribbean Sea)

Bary, Brian McKenzie
J 22(3): 823 (ostracod distribution)

Bass, smallmouth (*Micropterus dolomieui*)
J 22(3): 732 (in Bow River system, Alta.)

Bass, white (*Roccus chrysops*) (*Lepibema chrysops*)
B 149: 20, 123 (Great Lakes, catches)

Bathymaster leurolepis (*see* Ronquil)

Battle, Helen Irene
J 22(2): 289 (lamprey alimentary tract)

Bay of Islands, Nfld.
J 22(2): 599 (salmon investigations)

Beaton, Barbara
S 898 (blood of aquatic vertebrates)

Beaufort Sea
J 22(2): 543 (zooplankton)

Becker, Clarence Dale
J 22(5): 1175 (salmonid leech)

Behaviour
J 22(1): 173 (environmental, of coho fry)
(2): 369 (young Atlantic salmon to light gradients)
(4): 1035 (re ecology and interaction of young coho and trout)

Bell, Gordon Russell
S 934 (*in vivo* angiography)

Bella Coola area, B.C.
J 22(6): 1523 (pink salmon sea mortality rate estimation)

Belle Isle, Strait of
J 22(2): 433 (harp seal migration)

"Belly-burn"
J 22(4): 955 (re canning partially frozen salmon)

Berry, Richard James
J 22(4): 945 (juvenile winter flounder)

Bideford River, P.E.I.
J 22(3): 851 (Mn deposits on mud-snail shells)

Biely, Jacob
CVG 34 (effect of antioxidants on herring meal)
S 969 (antioxidant treatment of herring meal)

Bilinski, Edward
J 22(4): 891 (acetone in fish blood)

Bilton, Hebert Thomas
J 22(6): 1477 (salmon scale annuli)

Biomass
J 22(4): 945 (estimating theoretical, for winter flounder fishery)

Bishop, Daniel Magnus
J 22(4): 919 (sediment in streams)

Blair, Arthur Avery
J 22(2): 599 (Atlantic salmon)

Bligh, Emerson Graham
J 22(3): 861 (coloured scallop meats)
S 904 (research on quality processing and products)

Blood (*see also* Hemoglobin; Plasma; Serum)
J 22(3): 767 (electropherograms re salmonids and their hybrids for biochemical systematics)
(4): 891 (acetone bodies in salmonids)
(5): 1229 (clotting time of Atlantic cod)
S 898 (total volume in Atlantic cod)
934 (angiography of Pacific salmon)

Blubber
S 932 (fatty acid composition of lactating grey seal)
938 (NW. Atlantic seal industry)

Body proportions
J 22(2): 259 (rare Nfld. skates)

Bonavista, Nfld.
J 22(2): 465 (catch, age, and size trends in cod longlining)

Bonito, Pacific (*Sarda lineolata*)
J 22(3): 853 (in Strait of Georgia, B.C.)

Bordeleau, Michel André
J 22(1): 27 (carbonyl compounds in cod)

Bottles, drift (*see* Drift, determination of)

Bourne, Neil
J 22(2): 313 (scallop drags)
(3): 861 (coloured scallop meats)
(5): 1137 (paralytic shellfish poison)
S 910 (*Placopecten magellanicus*)

Boyd, John William
J 22(1): 53 (drip loss of frozen fish)
(1): 117 (tetracycline antibiotics)
(3): 849 (myxosporidian parasite)

Bras d'Or Lake area, N.S.
S 911 (limnology of barachois ponds)

Brawn, Vivien Mavis
J 22(6): 1555 (swimbladder volume of physoclists)

Brett, John Roland
J 22(2): 405 (pumpkinseed respiration)
(6): 1491 (relation of salmon weight to metabolism)
S 896 (young sockeye, swimming energy required)

Brill (Pacific) (*Eopsetta jordani*) (petrale sole)
S 922 (abundance measures from fisheries for several species)

British Columbia (*see also* Georgia, Strait of; Oceanography, B.C. coast; *also* specific localities)
S 892, 907, 959 (pulp-mill wastes disposal problems)

Brittlestars (echinoderms)
J 22(6): 1407 (bathymetric distribution off Oregon coast)

Brockerhoff, Hans
J 22(3): 643 (lysolecithinase of cod)
S 944 (stereospecific analysis of triglycerides)
967 (hydrolysis of triglycerides)

Browning, of flesh (Maillard browning)
J 22(3): 755 (after freeze-drying lingcod and sole)

Budde, W.
J 22(3): 865 (detection of cysts)

Bumpus, Dean Franklin
S 939 (sea-bed drifters)

Buoyancy
J 22(2): 335 (re young Atlantic salmon and trout swimbladder volume)

Buoys, transponding (*see* Drift)

Burbot (*Lota lota*)
J 22(3): 744 (in Bow River system, Alta.)

Burgher, Robert Douglas
S 945 (cod liver oil fatty acids)

Buss, Keen
J 22(5): 1261 (Esocidae hybrids)

Butler, Terrance Henry
J 22(5): 1305 (dusky sculpin)

C

Cabezon (*Scorpaenichthys marmoratus*)
J 22(1): 203 (biochemical systematics)

Caddisflies
S 966 (effect of DDT forest spraying in N.B.)

Cadmium compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)

Caesium compounds
S 941 (radioactive Cs^{137} seawater contamination)

Calanus finmarchicus (a copepod)
S 895 (deoxyribonucleic acids of)

Calanus glacialis (a copepod)
J 22(2): 543 (development rate, Canadian Arctic Ocean)

Calcium compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)
S 957 (in St. Lawrence River and Gulf sediments)

Caligus gurnardi (parasitic copepod)
S 951 (review and redescription of)

Calocaris (a decapod)
J 22(1): 1 (new species *C. templemani*)

Calycopsis nematophora (a medusa)
J 22(3): 841 (distribution and morphology, NE. Pacific)

Campbell, Neil John
S 888 (ICNAF research report, 1962)

Cancer magister (*see* Crab, Pacific edible)

Candling
J 22(3): 865 (trials for whitefish fillet tapeworm cysts)

Canning
J 22(4): 955 (partially frozen Pacific salmon)
CHN 22 (nature and control of sulphide discoloration)

Capelin (*Mallotus villosus*)
S 937 (*Pentagramma petrowi* trematode parasitism of Pacific)

Carassius auratus (*see* Goldfish)

Carbohydrates (*see also* Glycogen; Sugars)
B 125R: 151 (determination for sea water)

Carbon balance
J 22(4): 1083 (marine phytoplankton)

Carbon dioxide
B 125R: 37 (determination for sea water)

Carbonates
B 125R: 29 (determination for sea water)

Carbonyl compounds (*see also* Acid; Aldehydes; Carbohydrates; Ketones; Sugars)
S 921 (flame ionization detector response for carbonyl carbon)

Carcharhinus falciformis (*see* Shark, sickle)

Carcharhinus milberti (*see* Shark, sandbar)

Carcharhinus obscurus (*see* Shark, dusky)

Caribbean Sea
S 956 (Canadian fisheries research)

Carotenoids
S 923 (re marine-plant pigment determination)

Carp (*Cyprinus carpio*)
B 149: 22, 120 (Great Lakes, catches)

Carp (European)
J 22(6): 1397 (effort metabolism of lateral muscle)

Castell, Charles Howell
J 22(4): 929 (salt-induced rancidity)

Catch
J 22(1): 191 (solution of catch equation)
(2): 313 (scallops, by two drag-ring sizes)
(2): 465 (trends in Nfld. longlined cod)
B 149: 15, 111 (Great Lakes commercial)
CPO 1965-6 (NW. Strait of Georgia coho commercial troll)
CSG 44 (cod: distribution in Gulf of St. Lawrence)
S 922 (abundance measures from mixed)

Catfish, channel (*Ictalurus punctatus*)
B 149: 22 (Great Lakes, catches)

Catostomus catostomus (*see* Sucker, longnose)

Catostomus commersoni (*see* Sucker, white)

Cedar Lake, Man.
J 22(5): 1123 (limnological features)

Cestoda (*see* Tapeworms)

Chalker, Dorothy Ann
J 22(2): 411 (quality of frozen cod)
(3): 783 (thaw-drip in cod)

Chalkiness of fish flesh
J 22(3): 653 (Pacific halibut)

Chapman, Donald Wallace
J 22(1): 173 (coho behavior)

Chapman, Lyman John
J 22(4): 969 (Ontario crustaceans)

Char, Arctic (*Salvelinus alpinus*) (*Cristovomer alpinus*) (alpine trout)
J 22(1): 211 (retinal structure)
(3): 767 (and hybrids biochemical differentiation)

Char, Windermere (*Salvelinus alpinus willughbii*)
J 22(4): 913 (temperature re egg development and mortality rate)

Chew, Kenneth Kendall
J 22(4): 1099 (*Mytilicola orientalis*)

Chilipepper (*Sebastodes goodei*)
J 22(1): 231 (first B.C. record)

Chilling (*see also* Icing; Sea water, refrigerated; Refrigeration)
S 935 (fish on board vessels)

Chimaeridae
J 22(1): 203 (electropherograms re biochemical systematics)

Chitin
B 125R: 157 (determination for sea water)

Chlorophylls (*see also* Algae; Phytoplankton)
J 22(6): 1575 (*a*, *b*, *c*: nomographs for plankton pigment spectrophotometry)
B 125R: 125 (determination for sea water)
S 923, 924 (re marine-plant pigment determination)

Chlorophyta
J 22(3): 793 (phosphatase activity)
(4): 1083 (carbon balance)

Chlorosity (*see also* Salinity)
B 125R: 11, 183 (determination for sea water, tables)

Choline
S 933, 936 (fermentation by marine *Achromobacter*)

Chromatography, gas (*see* Acids, fatty)

Chrysophyta
J 22(3): 793 (phosphatase activity of some)
(4): 1083 (carbon balance)
(5): 1107 (lipid fatty acids)

Chub, lake (*Hybopsis plumbea*)
J 22(3): 742 (in Kananaskis River system, Alta.)
B 149: 21, 119 (Great Lakes, catches)

Cisco (*Coregonus artedii*) (*Leucichthys artedi*) (lake herring)
J 22(3): 732 (in Bow River system, Alta.)
B 149: 20, 119 (Great Lakes, catches)

Cisco, shortjaw (*Coregonus zenithicus*)
J 22(4): 969 (Algonquin Park, Ont., distribution)

Citric acid and citrates
J 22(1): 53 (for inhibiting drip loss)
(4): (re oxidative rancidity in cod flesh)
CVG 35 (acid, as antioxidant supplement)

Claggett, Freddie Gene
CVG 34 (effect of antioxidants on herring meal)
35 (spontaneous heating in herring meal)
S 969 (antioxidant treatment of herring meal)

Clam, softshell (Atlantic) (*Mya arenaria*)
S 909 (new hydraulic harvesting rake)

Clarke, Arthur Hadleton, Jr.
J 22(2): 631 (ancient sea shells)

Clupea harengus (*see* Herring, Atlantic)

Clupea pallasii (*see* Herring, Pacific)

Cobalt compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)
S 915 (vitamin B_{12} and cobamide coenzymes)
941 (radioctive Co^{60} seawater contamination)

Cod, Atlantic (biology) (*Gadus morhua*)
J 22(2): 421 ("sphyrion" type tag for)
(2): 465 (catch, age, size trends in Bonavista longlining)
(3): 643 (lengths, weights, liver and gonads weights)
(5): 1229 (blood-clotting time)
CSG 44 (catches distribution in Gulf of St. Lawrence)
S 886, 887, 890, 928, 930, 949, 955 (ICNAF research reports)
928 (catch size effect on otter trawl selectivity)
898 (total blood volume)
958 (impaired hormone metabolism in moribund)
970 (new fishing grounds off Labrador and NE. Nfld.)

Cod, Atlantic (products)
J 22(1): 13 (salting and smoking effects on protein quality)
(1): 17, 27 (carbonyl compounds re flavour of salted)
(1): 83 (glycolytic changes in muscle)
(2): 411 (quality re freezing rate of frozen stored trap cod)
(3): 643 (lysolecithinase in muscle)
(3): 783 (thraw-drip quality of treated and untreated fillets)
(4): 929 (pro- and antioxidant effects of various metal salts on lean muscle)
CHN 20 (identification of fillets by protein electrophoresis)
S 929 (protein concentrate processing and characteristics)
935 (chilling and freezing on board vessels)
945 (liver oil fatty acids as gas chromatography reference standards)

Cod, Pacific (*Gadus macrocephalus*)
J 22(1): 53 (drip and rancidity inhibitors)
(1): 203 (biochemical systematics)

Colour (*see* Pigmentation)

Columbia River
J 22(6): 1407 (brittlestars bathymetric distribution off mouth of)

Comer, Alan George
J 22(2): 307 (shrimp nucleotides)
S 894 (lingcod muscle enzymes)

Composition (biological)
S 952 (of Fraser River odd-year pink salmon run)

Conchoecia (ostracods)
J 22(3): 823 (diurnal and seasonal distribution changes)

Condition
J 22(4): 1099 (*Mytilicola* parasite effect on Pacific oyster)

Conroy, David Andrew
J 22(1): 243 (acid-fast bacteria)
(3): 869 (haematology of hake)

Conservation
S 899 (salmons in N. Pacific)

Contamination (*see* Bacteria; Pollution; Radioactivity)

Copepoda (*see also Calanus*)
J 22(2): 558 (development in Arctic Ocean)
(4): 969 (*Senecella* and *Limnocalanus* distribution, Algonquin Park, Ont.)
(6): 1335 (*Cyclops* infection by *Triaenophorus*)
S 951 (review and redescription of *Caligus gurnardi*)

Copper compounds
J 22(2): 425 (Cu–Zn pollutants lethal levels to salmon)
(4): 929 (inducing oxidative rancidity in cod muscle)
B 125R: 113 (determination for sea water)
S 931, 961 (toxicity towards Atlantic salmon)

Coregonus artedii (*see* Cisco)

Coregonus clupeaformis (*see* Whitefish, lake)

Coregonus zenithicus (*see* Cisco, shortjaw)

Cornea (*see* Eye)

Cortisol (*see* Hormones)

Coryphaenidae (*see* Dolphins)

Crab, king (*Paralithodes camtschatica*)
J 22(1): 101 (reproduction)
S 895 (deoxyribonucleic acids of)

Crab, Pacific edible
S 895 (deoxyribonucleic acids of)

Crassostrea gigas (*see* Oyster, Pacific)

Crassostrea virginica (*see* Oyster, Atlantic)

Cristovomer (*see Salvelinus*)

Crop, standing
J 22(2): 399 (brook trout re Ellerslie Brook siltiness)

Crossman, Edwin John
J 22(5): 1261 (Esocidae hybrids)

Crustacea (*see also* common names of species)
S 895 (deoxyribonucleic acids of)

Culeia inconstans (*see* Stickleback, brook)

Culture
S 943 (effect of serum on trout gonadal cells)

Curd, in canned fish
J 22(4): 955 (salmon and trout, partially frozen before canning)

Currents (*see also* Drift)
J 22(1): 225 (Fury and Hecla Strait, N.W.T.)
(2): 353 (Northumberland Strait drift)
(3): 689 (NE. Pacific Ocean)
(3): 801 (surface and tidal, re pollution removal)

Cyclops species (Copepoda)
J 22(6): 1335 (infections by *Triaenophorus* procercoids)

Cyprinus carpio (*see* Carp)

Cystophora cristata (*see* Seal, hooded)

Cysts
J 22(3): 865 (tapeworm, candling whitefish fillets for)
(6): 1345 (lymphocystis disease of American plaice)

D

Dace, blacknose (*Rhinichthys atronasus* (= *R. atratulus*))
J 22(3): 744 (in Bow River system, Alta.)

Dace, longnose (*Rhinichthys cataractae*)
J 22(3): 744 (in Kananaskis River system, Alta.)

Dale, Jacqueline
J 22(4): 875 (dimethyl-β-propiothetin)

Davenport, Douglas
J 22(5): 1309 (fish measurement)

Day, Lewis Rodman
J 22(2): 635 (killifish)
S 912 (salt-water system at St. Andrews Biological Station)

Daykin, Philip Norman
J 22(1): 159 (environment of fish eggs)

DDT (*see* Insecticides)

Decapoda (*see also* certain individual names of)
J 22(1): 1 (new species of *Calocaris*)
(1): 69 (Ungava Bay *Argis dentata* larvae and megalopa)

Dehydration (*see* Freeze-drying)

Denaturation (*see* Protein)

Denticles
J 22(4): 899 (use in identifying Atlantic skates)

Deoxyribonucleic acid (*see* Acids, nucleic)

Depth
S 908 (re size of lakes)

Dermochelys coriacea coriacea (*see* Turtle, leatherback)

Development rate (*see also* Growth)
J 22(2): 558 (Copepoda in Arctic Ocean)
(4): 913 (temperature effect on Windermere char eggs)
(6): 1567 (precocious sexual, in male Atlantic salmon)

Diaciuc, Ion Victor
J 22(6): 1397 (carp metabolism)

Diatoms (*see also* Bacillariophyta)
J 22(3): 793 (phosphatase activity of some marine)
(4): 1083 (carbon balance)
S 916 (of "red water" on west coast of India)

Dickie, Lloyd Merlin
J 22(2): 521 (growth of fishes)

Digestion
J 22(6): 1563 (degradation rate of organisms in, re feed studies)

Dimorphism
J 22(3): 697 (sexual, in immature sea lampreys)

Dinoflagellata
J 22(4): 1083 (carbon balance of "red tide" species)
S 916 (of "red water" on west coast of India)

Dinophyceae
J 22(5): 1107 (lipid fatty acids)

Discoloration (*see* Pigments)

Disease
J 22(3): 713 ("redmouth": oral immunization of trout)
(6): 1345 (lymphocystis of American plaice)

Dispersal (*see* Distribution; Migration; Movements)

Distribution (biological) (*see also* Migration; Movements; Species, new)
J 22(1): 139 (western brook lamprey)
(2): 259 (rare Nfld. skates)
(2): 621 (seasonal, monkfish)
(3): 721 (fishes in Kananaskis River system, Alta.)
(3): 823 (factors affecting diurnal and seasonal of two planktonic ostracods)
(3): 841 (and morphology of a NE. Pacific Medusa)
(4): 969 (some Algonquin Park crustaceans and fishes)
(5): 1151 (two species of N.E. Pacific Alepocephalidae)
(5): 1175 (freshwater leech parasitic on salmonids)
(6): 1391 (oceanic, of Pacific salmons traceable by parasites)
(6): 1407 (bathymetric, of Oregon coast brittlestars)
(6): 1425 (of intertidal algae re salinity and tides)
CSG 44 (Gulf of St. Lawrence cod catches)
S 925, 926 (NE. Pacific salmons)
968 (Canadian stoneflies)

Distribution (trade)
B 149: 45 (Great Lakes fisheries products)

Dogfish, Pacific (*Squalus suckleyi*)
J 22(1): 203 (biochemical systematics)

Dollinger, Edward Joseph
J 22(3): 653 (chalkiness in halibut)

Dolly Varden (*Salvelinus malma*)
J 22(3): 736 (in Kananaskis River system, Alta.)

Dolphins (Coryphaenidae)
S 956 (Canadian research in Caribbean Sea)

Doré (*see* Walleye)

Drags, drift (*see* Drift)

Drags, fishing
J 22(2): 313 (scallop catches by two ring-sizes of)

Drift, determination of (*see also* Currents)
J 22(1): 353 (Northumberland Strait, by bottles)
(3): 689 (NE. Pacific Ocean, by transponding buoys)
S 939 (seabottom, by weighted submerged draggers)

Drinnan, Roy Ellis
S 891 (water-pumping recording apparatus)

Drip
J 22(1): 53 (polyphosphate, citrate, and salt as inhibitors)
(4): 955 (after holding salmon in refrigerated sea water)

Driver, Edwin Andrew
J 22(5): 1165 (Manitoba saline lakes)

Drum, freshwater (*Aplodinotus grunniens*) (sheepshead)
B 149: 22, 123 (Great Lakes, catches)

Dryer, William Raymond
J 22(4): 999 (movement of trout in Lake Superior)

Dyer, William John
J 22(1): 83 (glycolytic activity in cod muscles)
(2): 411 (quality of frozen cod)

E

Echo sounding (*see* Sounding, echo)

Ecology
J 22(1): 173 (environmental and behavioural of juvenile coho)
(2): 565 (Magdalen Shallows American plaice)
(4): 1035 (re behaviour and interaction of young coho and trout)
(5): 1175 (of freshwater leech parasitic on salmonids)

Economics
B 149 (Great Lakes fisheries of Ontario)

Eels (Caribbean Sea)
S 956 (Canadian research)

Eggs, fish (*see also* Gonads; Spawning)
J 22(1): 159 (oxygen mass transport theory for fish)
(1): 247 (centrifugal subsampling re fecundity)
(4): 913 (temperature re mortality and development rate of char)
(6): 1503 (fertility retention in expressed sockeye)

Elasmobranchii (*see also* Dogfish; Shark; Skate)
J 22(1): 203 (electropherograms re biochemical systematics)

Electropherograms
J 22(1): 203, 215 (of fish components re biochemical systematics)
(3): 767 (of salmonid fishes and hybrids components re biochemical systematics)
CHN 20 (for distinguishing cod and haddock fillets)

Ellerslie Brook, P.E.I.
J 22(2): 395 (trout stream population re silt)

Elson, Paul Frederick
J 22(2): 421 (new toggle tag)
(2): 625 (Canadian salmon off Greenland)
S 920 (forest spraying)

Entosphenus lamottenii (*see* Lamprey, American brook)
Environment
J 22(1): 173 (effects on coho fry behaviour)
S 893, 905, 965 (re Atlantic salmon biology and management)
964 (mathematical analysis re aquatic pollution)
Enzymes
J 22(3): 643 (lysolecithinase in Atlantic cod muscle, and inhibitors)
(3): 793 (marine phytoplankters phosphatase activity)
S 894 (adenine-deaminating in lingcod muscle)
897 (mononucleotide synthesis by steelhead trout milt)
915 (structure and chemical reactions of cobamide coenzymes)
944 (in triglyceride stereospecific analysis)
967 (differential triglyceride hydrolysis by skate pancreatic lipase)

Eopsetta jordani (*see* Brill, Pacific)

Eppley, Richard Wayne
J 22(4): 1083 (phytoplankton photosynthesis)

Erie, Lake (*see also* Great Lakes)
J 22(5): 1197 (whitefish populations year-class fluctuations)

Erskine, John Steuart
J 22(2): 631 (ancient sea shells)

Esox americanus americanus (*see* Pickerel, redfin)

Esox americanus vermiculatus (*see* Pickerel, grass)

Esox lucius (*see* Pike, northern)

Esox masquinongy (*see* Maskinonge)

Esox niger (*see* Pickerel, chain)

Esters (*see* Acids, fatty; Lipids)

Eucalia inconstans (*see* Stickleback, brook)

Eulachon (*Thaleichthys pacificus*)
J 22(1): 203 (biochemical systematics)

Euphausids
J 22(5): 1107 (lipid fatty acids)

Exercise (*see* Activity)

Exocoetidae (*see* Flyingfishes)

Exploitation
S 952 (of Fraser River odd-year pink salmon run)

Exploration
S 901 (for fishery resources)
956 (Canadian re Caribbean Sea fisheries)
970 (new cod fishing grounds off Labrador and Nfld.)

Eye
J 22(1): 221 (Arctic char retinal structure)
(2): 513 (European flatfishes retinomotor changes)
(3): 761 (lake trout corneal lesions)

F

Fagerlund, Ulf Henrik Mathias
J 22(3): 775 (post-spawning death of salmon)

Fatigue (*see* Activity)

Fauna, bottom
J 22(5): 1123 (Cedar Lake, Man.)

Favorite, Felix
J 22(3): 689 (transponding oceanographic buoys)

Fecundity
J 22(1): 247 (centrifugal subsampling of fish eggs)

Feed
J 22(2): 265, 270 (of Nfld. rare skates)
(2): 521 (re growth curve of fishes)
(2): 575 (of American plaice)
(2): 608 (of Nfld. salmon)
(5): 1131 (*Limacina* snails affecting Pacific groundfish quality)
(6): 1357 (of Heming Lake, Man., northern pike)
(6): 1383 (photoperiod influence on metabolism in sunfish)
(6): 1563 (studies re digestive degradation rate in salmons)
B 149: 62 (pet and mink, from Great Lakes fisheries)
CVG 34, 35 (antioxidant value in preserving herring meal)
S 969 (antioxidant value in preserving herring meal)

Feeding, method of
S 891 (water-pumping behaviour of lamellibranchs)

Fertility (*see also* Fecundity; Hybrids)
J 22(6): 1503 (retention in expressed sockeye eggs and milt)

Fillets
J 22(2): 414 (cod: quality re freezing rate and storage)
(3): 783 (cod: thaw-drip quality, treated and untreated)
(3): 865 (lake whitefish: candling for tapeworm cysts)
CHN 20 (identification of cod and haddock by protein electrophoresis)

Fins
J 22(1): 219 (anomalies in white sucker)
(1): 237 (abnormalities in thorny skate)
(6): 1345 (lymphocystis disease of American plaice)

Fish flour (*see* Protein concentrate)

Fishing methods (*see also* Catch; Gear; Vessels)
S 903 (Canadian research on improvements for)

Fishmeals
CVG 34 (antioxidant value in improving nutritive value of herring meal)
S 969 (antioxidant value in improving nutritive value of herring meal)

Fisk, Donald
J 22(3): 689 (transponding oceanographic buoys)

Flavour of products (*see* Quality of products)

Fleming, Allister Melville
J 22(2): 465 (Bonavista commercial cod fishery)

Flesh (*see also* Chalkiness; Fillets)
J 22(3): 755 (browning of freeze-dried lingcod and sole)
(4): 955 (colour and firmness in salmon canned after partial freezing)

Flounder, arrowtooth (*Atheresthes stomias*)
J 22(1): 203 (biochemical systematics)

Flounder, starry (*Platichthys stellatus*)
J 22(1): 203 (biochemical systematics)

Flounder, winter (*Pseudopleuronectes americanus*)
J 22(4): 945 (estimating theoretical juvenile biomass for a fishery)

Flounder, witch (*Glyptocephalus cynoglossus*) (greysole)
J 22(6): 1565 (new size record)
S 949, 955 (ICNAF research reports)

Flour, fish (*see* Protein concentrate)

Flukes (Trematoda)
J 22(6): 1387 (re Pacific salmons biological information)
S 937 (review of *Bacciger* and *Pentagramma*; *P. petrowi* from B.C. marine fishes)

Flyingfishes (Exocoetidae)
S 956 (Canadian research in Carribbean Sea)

Foams
S 892, 907 (re pulp-mill pollutive effects)

Foerster, Russel Earle
J 22(6): 1503 (fertility of salmon)

Follett, Wilbur Irving
J 22(1): 139 (*Lampetra richardsoni*)

Food, of animals (*see* Feed)

Fraser, Doris Isabel
J 22(1): 83 (glycolytic activity in cod muscle)

Fraser River system, B.C.
J 22(4): 1035 (young coho and steelhead trout behaviour re ecology in lower tributaries)
S 952 (migration, composition, exploitation, abundance, of pink salmon odd-year run)

Fredin, Reynold Allen
J 22(1): 33 (ocean mortality of salmon)

Freeman, Harry Cleveland
S 858 (impaired hormone metabolism)

Freeze-drying and freeze-dried products
J 22(3): 755 (browning of flesh)

Freezing
J 22(2): 411 (rate effect on stored frozen trap cod)
(3): 783 (effect on cod fillet thaw-drip)
(4): 955 (partial, to preserve salmon before canning)
S 935 (fish on board vessels)

Frick, Harold Clay
B 149 (Great Lakes fisheries economics)

Fromm, Paul Oliver
J 22(3): 761 (keratitis in lake trout)
(6): 1379 (photoperiod effects on sunfish)

Fry
J 22(1): 173 (behaviour of coho salmon)

Fundulus diaphanus (*see* Killifish, banded)

Fundulus heteroclitus (*see* Mummichog, common)

Fury and Hecla Strait, N.W.T.
J 22(1): 225 (current speed and direction)

G

Gadd, Ronald Edward Alfred
J 22(3): 755 (freeze-dried fish)

Gadus macrocephalus (*see* Cod, Pacific)

Gadus morhua (*see* Cod, Atlantic)

Galeocerdo cuvieri (*see* Shark, tiger)

Gambia affinis (*see* Mosquitofish)

Gear, fishery (*see also* types of gear)
B 149: 65 (Great Lakes commercial fisheries)
S 903 (Canadian improvement research)
928, 940, 949, 954, 955 (ICNAF research reports)
909 (softshell clam hydraulic harvesting rake)

Geiger, Shirley Evelyn
J 22(3): 653 (chalkiness in halibut)
(4): 955 (partial freezing of salmon)

S 947 (sodium, potassium, and magnesium in fish)

Geology
S 908 (Canadian large lakes)
953 (Gulf of St. Lawrence marine)
957 (St. Lawrence River and Gulf recent depositional conditions)

Georgia, Strait of
J 22(3): 853 (Pacific bonito characteristics)
CPO 1965-2 (monthly mean surface temperatures, 1964)
1965-3,5,7,8 (oceanographic cruises reports)
1965-6 (commercial coho troll catches)

Glycerides (*see* Acids, fatty; Lipids)

Glycogen; glycolysis
J 22(1): 83 (post-mortem changes in cod muscle)
(6): 1397 (in carp lateral muscle effort metabolism)

Glyptocephalus cynoglossus (*see* Flounder, witch)

Glyptocephalus zachirus (*see* Sole, rex)

Goldfish (*Carassius auratus*)
J 22(6): 1455 (thermal effects on ionic regulation)

Gonads (*see also* Eggs; Milt)
J 22(3): 643 (proportion and lysolecithinase activity in cod)
(3): 697 (histology in immature sea lampreys)
(5): 1137 (*Gonyaulax* toxicity in scallop)
S 943 (cells of rainbow trout, growth stimulation by serum)
962 (salmon pituitary hormones effect on immature trout)

Gonyaulax (protozoan flagellates) (*see* Shellfish toxicity)

Grainger, Edward Henry
J 22(2): 543 (Arctic zooplankton)

Great Bear Lake, N.W.T.
S 908 (limnology)

Great Lakes (*see also* Erie, Lake; Huron, Lake; Superior, Lake)
J 22(2): 289 (comparison of lampreys alimentary tracts)
(5): 1197 (whitefish populations year-class fluctuations)
B 149 (economic aspects of Ontario fisheries: species, gear, catches, etc.)
S 900 (availability of fishes)
908 (limnology)

Great Lakes Fisheries Commission
B 149: 92 (history)

Great Slave Lake, N.W.T.
J 22(6): 1571 (fall domestic fishery at Snowdrift)
S 900 (availability of fishes)
908 (limnology)
946 (1945–63 fishing fleet)

Greenfield, David Wayne
J 22(3): 857 (six-gilled shark)

Greenland
J 22(2): 422 (Canadian-tagged harp seal recaptures)

Greenling, whitespotted (*Hexagrammos stelleri*)
J 22(1): 203 (biochemical systematics)

Greysole (*see* Flounder, witch)

Gribbles (*Limnoria* isopod wood-borers)
S 948 (indigenous *L. lignorum* and introduced *L. tripunctata* on B.C. coast)

Grinols, Richard Byron
J 22(5): 1151 (Pacific Alepocephalidae)

Groot, Cornelis
J 22(4): 1025 (recording fish movements)

Gross, Willard Louis
J 22(6): 1379 (photoperiod effects on sunfish)

Grosslein, Marvin Darrel
S 940 (haddock off N.S.)

Groundfish, Atlantic
CJG 12 (landings in Nfld.)
S 886, 887, 890, 928, 930, 940, 949, 954, 955 (ICNAF research reports)

Growth (*see also* Development rate)
J 22(2): 281 (effect of light for Atlantic oyster, mussel, quahaug)
(2): 521 (curves and equations re feed of fishes)
(2): 568 (rate, American plaice)
(5): 1229 (and morphometry of four B.C. pygmy whitefish populations)
(6): 1379 (photoperiods influence on green sunfish)

H

Haddock (biology) (*Melanogrammus aeglefinus*)
S 886, 887, 890, 928, 930, 940, 949, 955 (ICNAF research reports)
928 (catch size effect on otter trawl selectivity)
940 (abundance, age composition of landings, mortality; off N.S.)

Haddock (products)
CHN 20 (identification of fillets by protein electrophoresis)

Haight, Conrad Giles
J 22(6): 1571 (fall fishery at Snowdrift, N.W.T.)

Hake (Argentine) (*Merluccius merluccius hubbsi*)

J 22(3): 869 (hematological study)

Hake, Pacific (*Merluccius productus*)
J 22(5): 1107 (liver lipid fatty acids)

Halibut, Pacific (*Hippoglossus stenolepis*)
J 22(1): 53 (drip and rancidity inhibitors)
(1): 203 (biochemical systematics)
(3): 653 (flesh chalkiness)

Halichoerus grypus (*see* Seal, grey)

Hammerhead, scalloped (*Sphyrna lewini*)
S 956 (Canadian research in Caribbean Sea)

Harling, Wayne Robert
J 22(5): 1309 (fish measurement)

Hart, John Lawson
J 22(2): 255 (an appreciation of A. G. Huntsman)

Hartman, Gordon Fredrick
J 22(4): 1035 (behavior of salmon and trout)

Hatchetfish (*Polyipnus asteroides*)
J 22(5): 1303 (range extension for W. Atlantic)

Hayashida, Kaye
J 22(2): 289 (lamprey alimentary tract)

Heat exchange in waters
J 22(6): 1321 (along Canadian Maritimes coast)

Heinicke, Elizabeth Anne
J 22(6): 1455 (thermal acclimation of goldfish)

Hemilepidotus spinosus (*see* Irish lord, brown)

Heming Lake, Man.
J 22(1): 219 (white sucker fin anomalies)
(6): 1357 (pike feed)

Hemoglobin (*see also* Blood)
J 22(1): 203, 215 (electropherograms re fish biochemical systematics)
(3): 869 (hematology of an Argentine hake)

Henderson, Eugene Blair
J 22(6): 1567 (Atlantic salmon development)

Hennemuth, Richard Clark
S 940 (haddock off N.S.)

Herring, Atlantic (*Clupea harengus*)
S 887, 955 (ICNAF research reports)
929 (protein concentrate processing and characteristics)
950 (water temperature re Isles-de-la-Madeleine fishery)

Herring, lake (*see* Cisco)

Herring, Pacific (biology) (*Clupea pallasii*)
J 22(1): 203 (biochemical systematics)
S 937: 394 (*Pentagramma petrowi* trematode parasitism)

Herring, Pacific (products)
CVG 34 (value of antioxidants in improving meal nutritive value)
35 (antioxidant control of meal spontaneous heating)
S 969 (value of antioxidants in improving meal nutritive value)

Hexagrammos stelleri (*see* Greenling, white-spotted)

Hexanchus corinus (*see* Shark, sixgill)

Hexanchus griseus (*see* Shark, sixgill)

Heyamoto, Hiromu
J 22(5): 1151 (Pacific Alepocephalidae)

Hippoglossoides elassodon (*see* Sole, flathead)

Hippoglossoides platessoides (*see* Plaice, American)

Hippoglossus stenolepis (*see* Halibut, Pacific)

Histology
J 22(1): 221 (Arctic char retina)
(2): 289 (lampreys intraperitoneal intestinal tract)
(2): 475 (stoneflies)
(2): 513 (eye of flatfishes)
(3): 695 (immature sea lamprey gonads)
(3): 761 (lake trout corneal lesions)
(3): 775 (some organs of post-spawned sockeye)
(6): 1345 (lymphocystis disease of American plaice)

History (*see also* Life history)
B 149: 89 (Great Lakes fisheries regulations and Commission),
143 (fisheries development on each of Great Lakes)

Hodder, Vincent Mackay
CJG 12 (Nfld. groundfish landings)
S 906 (Nfld. squid fishery)
928 (selectivity of otter trawls)

Hoffert, Jack Russell
J 22(3): 761 (keratitis in lake trout)

Hogenkamp, Henricus Petrus Cornelis
S 915 (cobamide coenzyme structure)

Holland, Gilbert Arthur
S 952 (odd-year pink salmon in the IPSFC Convention Area)

Hollister, Henry John
CPO 1965-2 (surface seawater temperatures)
1965-4 (seawater salinities)

Homarine
J 22(2): 307 (in pink shrimp)

Homarus americanus (*see* Lobster)

Hormones
S 958 (impaired metabolism in moribund Atlantic cod)
962 (salmon pituitary hormones effect on immature trout gonads)

Horton, Donald B.
J 22(4): 945 (juvenile winter flounder)

Hourston, Alan Stewart
S 952 (odd-year pink salmon in the IPSFC Convention Area)

Houston, Arthur Hillier
J 22(6): 1455 (thermal acclimation of goldfish)

Hoyle, Richard James
S 967 (hydrolysis of triglycerides)

Humber River, Nfld.
J 22(2): 599 (salmon investigations)

Huntsman, Archibald Gowanlock
J 22(2): 255 (an appreciation of)

Huron, Lake (*see also* Great Lakes)
J 22(5): 1197 (whitefish populations year-class fluctuations)

Hybopsis plumbea (*see* Chub, lake)

Hybrids
J 22(3): 732 (cutthroat × rainbow trouts), 743 (lake chub × longnose dace)
(3): 767 (between *Salmo, Salvelinus, Cristovomer*: biochemical differentiation)
(5): 1261 (between pickerels, pike, and maskinonge)

Hydrography (*see also* Oceanography)
S 886, 887, 888, 949, 955 (ICNAF research reports)
956 (Caribbean Sea)

Hydrolagus colliei (*see* Ratfish)

Hypomesus pretiosus (*see* Smelt, surf)

I

Icelinus burchami (*see* Sculpin, dusky)

Ichthyomyzon fossor (*see* Lamprey, northern brook)

Ichthyomyzon unicuspis (*see* Lamprey, silver)

Icing
S 935 (fish on board vessels)

ICNAF (*see* International Commission for the Northwest Atlantic Fisheries)

Ictalurus punctatus (*see* Catfish, channel)

Ide, Frederick Palmer
S 963 (Nymphomyiidae)
966 (effects of forest spraying)

Idler, David Richard
J 22(2): 411 (quality of frozen cod)
(3): 783 (thaw-drip in cod)
S 958 (impaired hormone metabolism)

Illex illecebrosus (*see* Squid, Newfoundland)

Illumination (*see* Light, reactions to)

India
S 916 ("red water" occurrence on west coast)

Indian Arm, B.C.
J 22(3): 823 (diurnal and seasonal distribution changes of two planktonic ostracods)

Ingraham, Woodrow James, Jr.
J 22(3): 689 (transponding oceanographic buoys)

Injury
J 22(2): 639 (lobster abdominal membrane lesions)
S 910 (shell repair by sea scallops)

INPFC (*see* International North Pacific Fisheries Commission)

Insecticides
J 22(2): 503 (DDT effect on young Atlantic salmon temperature selection)
S 893, 905, 920, 965 (DDT forest spraying effects on Atlantic salmon and trouts)
966 (DDT effect on aquatic insects)

Insects, aquatic
J 22(2): 475 (new species and records of stoneflies)
S 963 (new genus of Nymphomyiidae found in N.B.)
966 (effect of DDT forest spraying in N.B.)

Insolation (*see also* Photosynthesis)
S 919 (re cloud amount and sun altitude over ocean)

Interaction
J 22(4): 1035 (between underyearling coho and steelhead trout)

International Commission for the Northwest Atlantic Fisheries (ICNAF)
S 886, 887, 888, 890, 949, 955 (Canadian research participation reports re groundfish; other commercial species; gear; hydrography)
928 (catch size effect on otter trawls selectivity)
940 (N.S. haddock abundance, age, mortality)
954 (minimum mesh size data re regulations)

International North Pacific Fisheries Commission (INPFC)
S 925, 926 (Canadian research progress, 1962, 1963)

International Pacific Salmon Fisheries Commission (IPSFC)
S 952 (migration, composition, exploitation, abundance, of Fraser River odd-year pink salmon runs)

Intestine
J 22(3): 775 (histology, of post-spawned sockeye)

IPSFC (*see* International Pacific Salmon Fisheries Commission)

Irish lord, brown (*Hemilepidotus spinosus*)
J 22(1): 203 (biochemical systematics)

Iron compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)
B 125R: 97 (determination for sea water)
S 941 (radioactive Fe^{55} seawater contamination)

Iles-de-la-Madeleine, Gulf of St. Lawrence
S 950 (water temperatures re herring fishery)

Isopsetta isolepsis (*see* Sole, butter)

Isotopes
S 941 (radioactive, as seawater contaminants)

Isurus oxyrhinchus (*see* Mako)

J

Jackfish (*see* Pike, northern)

Jangaard, Peter Michael
J 22(1): 131 (lipids of squid)
CHN 22 (sulphide discoloration ("smut"))
S 932 (grey (Atlantic) seal)

Jean, Yves Marie Louis
J 22(2): 621 (Canadian Atlantic monkfish)

Johnson, Lionel
J 22(1): 239 (salinity of Baker Lake, N.W.T.)

Jonas, Richard Edmund Ernest
J 22(4): 891 (acetone in fish blood)

K

Kananaskis River system, Alta.
J 22(3): 721 (fish introduction and dams re fishes of)

Katkansky, Stanley Charles
J 22(4): 1099 (*Mytilicola orientalis*)

Katz, Max
J 22(5): 1175 (salmonid leech)

Kay, William Wayne
J 22(4): 955 (partial freezing of salmon)
S 947 (sodium, potassium, and magnesium in fish)

Keleher, James John
J 22(6): 1571 (fall fishery at Snowdrift, N.W.T.)
S 946 (Great Slave Lake fishing fleet)

Kerswill, Charles James
J 22(2): 281 (shellfish growth)
(2): 625 (Canadian salmon off Greenland)
S 920 (DDT forest spraying in N.B.)

Ketchen, Keith Stuart
S 922 (measures of species abundance for certain fisheries)

Ketones
J 22(1): 17 (identification re salted cod flavour)
(4): 891 (acetoacetate and β-hydroxybutyrate in salmonid blood)

Keys
J 22(2): 475 (stonefly species)
(5): 1296 (*Bathymaster* ronquil species)

Killifish, banded (*Fundulus diaphanus*) (freshwater mummichog)
J 22(2): 635 (probable toxicity to warm-blooded animals)

King, George Robert
J 22(4): 999 (movement of trout in Lake Superior)

Klontz, George William
J 22(3): 713 (redmouth disease)

Kohler, Allan Carl
CSG 46 (St. Lawrence cod fishery)
S 956 (fisheries research in Caribbean Sea)

Kokanee (*Oncorhynchus nerka*) (landlocked sockeye salmon)
J 22(3): 665 (factors affecting spawning entry into a lake tributary)

L

Labrador
S 970 (new cod fishing grounds off coast)

Lactic acid
J 22(4): 891 (in exercised salmonids)
(6): 1397 (in carp lateral muscle effort metabolism)

Laishley, Edward
J 22(2): 411 (quality of frozen cod)

Lakes (*see also* Limnology *and* names of individual lakes)

S 900 (large Canadian, re availability of fish)
908 (large Canadian: physiography and limnology)

Lakes, saline
J 22(5): 1165 (limnology of west-central Manitoba)
S 911 (limnology of Bras d'Or Lake area barachois ponds)

Lampetra lamottei (*see* Lamprey, American brook)

Lampetra richardsoni (*see* Lamprey, western brook)

Lamprey, American brook (*Lampetra lamottei*) (*Entosphenus lamottenii*)
J 22(2): 289 (alimentary tract comparative study)

Lamprey, Michigan brook (*see* Lamprey, northern brook)

Lamprey, northern brook (*Ichthyomyzon fossor*) (Michigan brook lamprey)
J 22(2): 289 (alimentary tract comparative study)

Lamprey, sea (*Petromyzon marinus*)
J 22(2): 289 (alimentary tract comparative study)
(3): 695 (sexual ratios and dimorphism in immature)
B 149: 104 (effect on Great Lakes fisheries; control)

Lamprey, silver (*Ichthyomyzon unicuspis*)
J 22(2): 289 (alimentary tract comparative study)

Lamprey, western brook (*Lampetra richardsoni*) (*L. planeri*)
J 22(1): 139 (distinguished as new non-parasitic species)

Landings
CJG 12 (groundfish in Nfld.)

Lanternfishes (Myctophidae)
S 956 (Canadian research in Caribbean Sea)

Larkin, Peter Anthony
S 908 (large Canadian lakes physiography and limnology)

Larvae
J 22(1): 69 (of decapod *Argis dentata*)
(5): 1313 (of W. Atlantic sandlances)

Lauzier, Louis Marcel
J 22(2): 353 (drift bottle observations)
(6): 1321 (marine climate comparisons)
S 888 (ICNAF research report, 1962)
939 (sea-bed drifters)
950 (water temperature and herring fishing)
956 (fisheries research in Caribbean Sea)

Lawler, George Herbert
J 22(1): 219 (white sucker fin anomalies)
(5): 1197 (Lake Erie whitefish)
(6): 1335 (natural infections of cyclopid copepods)
(6): 1357 (food of the pike)

LeBrasseur, Robin John
J 22(6): 1563 (degradation of consumed organisms)

Lecithin
CVG 35 (as antioxidant supplement)

Lee, Arthur James
S 939 (sea-bed drifters)

Leech, salmonid (*Piscicola salmositica*)
J 22(5): 1175 (distribution, ecology, biology)

Lei Ching, Hilda
S 937 (*Bacciger* and *Pentagramma*)

Length (*see also* Length-weight ratio; Size)
J 22(5): 1309 (new type of board for measuring length frequencies)

Length-weight ratio
J 22(3): 702 (immature sea lampreys)

Lepibema chrysops (*see* Bass, white)

Lepidopsetta bilineata (*see* Sole, rock)

Lepomis cyanellus (*see* Sunfish, green)

Lepomis gibbosus (*see* Pumpkinseed)

Lesions (*see also* Injury)
J 22(3): 761 (corneal, in hatchery lake trout)

Lesser Slave Lake, Alta.
S 900 (availability of fishes)

Leucichthys species (*see* Cisco)

Leung, Tat Chi
CHN 20 (identification of fillets)

Li, Ming Fang
S 943 (growth of rainbow trout)

Life history
J 22(2): 565 (American plaice in Magdalen Shallows)

Light, and reactions to
J 22(2): 281 (effect on growth of Atlantic oyster, mussel, quahaug)
(2): 369 (young Atlantic salmon behaviour to photoperiods and gradients)
(3): 825 (gradients re marine ostracod distribution)
(6): 1379 (photoperiods influence on green sunfish growth)

Limacina helicina (marine planktonic snail)
J 22(5): 1311 (in feed of B.C. groundfish affects quality)

Limnocalanus macrurus (a copepod)
J 22(4): 969 (Algonquin Park, Ont., distribution)
Limnology
J 22(3): 665 (Nicola Lake, B.C.)
(5): 1123 (Cedar Lake, Man.)
(5): 1165 (saline west-central Manitoba lakes)
S 900 (Canadian lakes re availability of fish)
908 (Canadian large lakes)
911 (barachois ponds in Bras d'Or Lake area, N.S.)

Limnoria (*see* Gribbles)

Lingcod (*Ophiodon elongatus*)
J 22(1): 203 (biochemical systematics)
(3): 755 (browning of freeze-dried flesh)
S 894 (muscle adenine deamination enzymes)

Lipids (*see also* Acids, fatty)
J 22(1): 131 (of Nfld. squid)
(3): 643 (lysolecithinase action on cod phospholipids)
B 125R: 147 (determination for sea water)
CVG 34 (energy value in herring meal)
35 (oxidation causing heating of fish meals)
S 944 (stereospecific analysis of triglycerides)
967 (triglycerides hydrolysis by skate pancreatic lipase)

Lippa, Erich Johannes Richard
J 22(5): 1311 (contamination of groundfish)

Lithium compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)
Liver
J 22(1): 131 (lipids and component fatty acids of squid)
(3): 643 (percentage and lysolecithinase activity in cod)
(3): 775 (histology, of post-spawned sockeye)
(5): 1107 (lipid fatty acids of Pacific hake and whiting)
(5): 1137 (*Gonyaulax* toxicity in scallop)
S 945 (Atlantic cod: oil fatty acids)

Lobster (*Homarus americanus*)
J 22(2): 385 (survival out of water)
(2): 421 (toggle tag new design)
(2): 639 (abdominal membrane lesions)
(4): 1103 (*Anonyx* parasite of)
CHG 21 (unit for holding and displaying live)
CSG 45 (handling and shipping care for live)
S 927 (oxygen consumption)

Longlining
J 22(2): 465 (cod: catch, age, size)

Lophius americanus (*see* Monkfish)

Loring, Douglas Howard
S 953 (geological investigations in the Gulf of St. Lawrence)
957 (depositional conditions in the St. Lawrence region)

Lorz, Harold William
J 22(3): 665 (movement of mature kokanee)
Lota lota (*see* Burbot)

Lumpenus sagitta (*see* Prickleback, snake)

Lutjanus species (*see* Snappers)

M

MacCallum, Wallace Allison
J 22(2): 411 (quality of frozen cod)
(3): 783 (thaw-drip in cod)
S 935 (chilling and freezing fish on board vessels)

MacLaren, Alethea
B 149: 143 (history of Great Lakes fisheries)

MacLean, Jill
J 22(4): 929 (salt-induced rancidity)

Macnab, Heather Claire
J 22(5): 1299 (blood clotting in cod)
S 898 (blood of aquatic vertebrates)

MacPhail, John Stuart
S 909 (new hydraulic clam rake)

Magdalen Shallows, Gulf of St. Lawrence
J 22(2): 565 (life history of American plaice)

Magnesium compounds
J 22(1): 113 (seawater Mg ion activity coefficient)
(1): 117 (re antibiotic bacteria inhibitors)
(4): 929 (re oxidative rancidity promotion in cod flesh)
(4): 955 (Mg ion change in salmon held in refrigerated sea water)
S 947 (Mg ion changes in fish held in refrigerated sea water)

Maillard browning (*see* Browning, of flesh)

Mako (*Isurus oxyrhinchus*)
S 956 (Canadian research in Caribbean Sea)

Malacostraca
J 22(4): 969 (*Mysis* and *Pontoporeia* distribution in Algonquin Park, Ont.)

Mallotus villosus (*see* Capelin)

Management (*see also* International Commission for the Northwest Atlantic Fisheries; International North Pacific Fisheries Commission; International Pacific Salmon Fisheries Commission)
S 893 (Atlantic salmon and brook trout research program, 1962–63)
902 (of fisheries populations for fisheries development)

Manganese compounds
J 22(3): 851 (deposit on mud-snail shells, P.E.I.)
B 125R: 107 (determination for sea water)
S 941 (radioactive Mn^{54} seawater contamination)

Manitoba (*see also* certain individual localities, e.g. Heming Lake)
J 22(5): 1123 (Cedar Lake limnology)
(5): 1165 (west-central saline lakes Classification)

Mann, David Seymour
S 912 (salt-water system at St. Andrews Biological Station)

Mantle (of shellfishes)
J 22(5): 1137 (*Gonyaulax* toxicity in scallops)

Manzer, James Ivan
J 22(3): 853 (Strait of Georgia bonito)

March, Beryl Elizabeth
CVG 34 (effect of antioxidants on herring meal)
S 969 (antioxidant treatment of herring meal)

Marcotte, Alexandre
J 22(6): 1321 (marine climate comparisons)
CSG 44 (distribution of cod catches)

Margolis, Leo
J 22(6): 1387 (parasites as biological indicators)
S 937 (*Bacciger* and *Pentagramma*)

Markert, John Richard
J 22(1): 215 (*Oncorhynchus*, species identification)

Markets
B 149: 25 (Great Lakes fisheries products)

Marking
J 22(6): 1477 (pink salmon for comparing scale age)
(6): 1523 (pink salmon for sea mortality rate estimation)

Martin, Nigel Vernon
J 22(4): 969 (Ontario crustaceans)

Martin, William Robert
S 887 (ICNAF research report, 1962)
903 (research on improvement of fishing methods)

Maskinonge (*Esox masquinongy*) (muskellunge)
J 22(5): 1261 (hybrids with other Esocidae)

Mason, John Christopher
J 22(1): 173 (coho behavior)

Masu (*Oncorhynchus masou*) (masu salmon)
S 899 (ocean stocks and fishery developments)

Mathematical treatment
J 22(1): 33 (estimating Pacific salmons ocean mortality)
(1): 159 (oxygen mass transfer re fish-egg respiration)
(1): 191 (catch equation)
(2): 521 (growth curve of fishes)
(4): 945 (estimating theoretical biomass for a fishery)
(6): 1523 (pink salmon sea mortality rate estimation)
B 125R: 5 (statistical limits in sea water analyses)
S 959 (pulpmill effluent sedimentation)
964 (analysis of experimental multivariable environments re aquatic pollution)

Matter, particulate, in natural waters
J 22(5): 1107 (marine lipid fatty acids)
B 125R: 117 (determination for sea water)

Maturity
S 925, 926 (re age of NE. Pacific salmons)

May, Arthur William
S 928 (selectivity of otter trawls)
970 (new cod fishing grounds)

Mayflies
S 966 (effect of DDT forest spraying in N.B.)

McAllister, Donald Evan
J 22(6): 1559 (widow rockfish)

McBride, John Raymond
J 22(3): 775 (post-spawning death of salmon)

McCart, Peter
J 22(5): 1229 (pygmy whitefish)

McCracken, Francis Derwood
CSG 44 (distribution of cod catches)
S 930 (future of groundfishing industry)
940 (haddock off Nova Scotia)
954 (minimum mesh sizes)

McHardy, Robert Alexander
J 22(3): 823 (ostracod distribution in B.C.)

McLeese, Donald Wilson
J 22(2): 385 (lobster survival in air)
(2): 639 (lesions on lobsters)
S 912 (salt-water system at St. Andrews Biological Station)
927 (oxygen consumption of the lobster)

McPhail, John Donald
J 22(5): 1293 (new ronquil from Aleutian Islands)

Meals, fish (*see* Fishmeals)

Medcof, John Carl
J 22(2): 281 (shellfish growth)
(2): 631 (ancient sea shells)
(2): 635 (killifish)
S 909 (new hydraulic clam rake)
910 (*Placopecten magellanicus*)
955 (ICNAF research areas)

Medusa
J 22(3): 841 (*Calycopsis nematophora* distribution and morphology in NE. Pacific Ocean)

Megalopa
J 22(1): 69 (of decapod *Argis dentata*)

Melanogrammus aeglefinus (*see* Haddock)

Menominee (*see* Whitefish, round)

Mercenaria mercenaria (*see* Quahaug)

Meristic characteristics (*see also* Species, new)
J 22(3): 853 (Strait of Georgia Pacific bonito)
(4): 899 (in distinguishing little from winter skate)
(6): 1559 (widow rockfish)

Merluccius merluccius hubbsi (*see* Hake (Argentine))

Merluccius productus (*see* Hake, Pacific)

Mesh (*see* Nets)

Metabolism
J 22(6): 1372 (re size of northern pike and its feed)
(6): 1397 (effort in carp lateral muscle)
(6): 1491 (O_2 consumption re sockeye swimming speed and size)
CVG 34 (metabolizable energy of herring meal)
S 896 (respiratory of swimming young sockeye)
958 (moribund Atlantic cod impaired hormone)
969 (metabolizable energy of herring meal)

Michigan, Lake (*see* Great Lakes)

Microcalanus pygmaeus (a copepod)
J 22(2): 543 (development rate in Canadian Arctic Ocean)

Micropterus dolomieui (*see* Bass, smallmouth)

Microstomus kitt (*see* Sole, merry)

Microstomus pacificus (*see* Sole, Dover)

Migration (*see also* Distribution; Movements; Spawning; Tagging)
J 22(2): 433 (NW. Atlantic harp seals)
(2): 625 (Canadian and European salmon to Greenland)
(4): 1025 (recording sockeye smolt movements by time-lapse photography of sonar traces)
S 952 (of Fraser River odd-year pink salmon run)

Miller, Bruce
J 22(3): 857 (six-gilled shark)

Milt (*see also* Gonads)
J 22(6): 1503 (sperm fertility retention from expressed sockeye)
S 897 (mononucleotide synthesis by extract of steelhead trout)

Minnow, flathead (*Pimephales promelas*)
J 22(3): 744 (in Bow River system, Alta.)

Mitchell, Barbara Susan
S 962 (pituitary hormones of salmon)

Mollusca
J 22(4): 977 (records from NW. Atlantic, 1946–61)

Monkfish (*Lophius americanus*)
J 22(2): 621 (Canadian Atlantic inshore distribution)

Moore, Barbara
J 22(4): 929 (salt-induced rancidity)

Morphology (*see also* names of organisms, organs, and tissues)
J 22(3): 841 (and distribution of NE. Pacific *Calycopsis nematophora*)

Morphometry (*see also* Range, extension of; Species, new)
J 22(3): 857 (San Juan Islands six-gill shark)
(5): 1229 (re pygmy whitefish growth)
(6): 1559 (widow rockfish)
S 951 (*Caligus gurnardi* parasitic copepod)

Morrison, Alexander Baillie
J 22(1): 13 (protein quality of cod)

Mortality, freshwater
J 22(4): 913 (temperature effect on Windermere char eggs)

Mortality, ocean
J 22(1): 33 (estimating for sockeye salmon; applications)
(2): 597 (re cod predation on American plaice)
(6): 1523 (rate in pink salmon)
S 940 (total, southern N.S. haddock)
910 (causes of natural and fishing, sea scallops)

Mosquitofish (*Gambia affinis*)
J 22(3): 732 (in Bow River system, Alta.)

Moulting
J 22(2): 453 (harp seals)

Mousette, Marcel
CSG 44 (distribution of cod catches)

Movements (*see also* Distribution; Migration)
J 22(4): 999 (of hatchery-reared lake trout in Lake Superior)

Mummichog, common (*Fundulus heteroclitus*)
J 22(2): 635 (probable toxicity to warm-blooded animals)

Mummichog, freshwater (*see* Killifish, banded)

Munro, Ian Craig
J 22(1): 13 (protein quality of cod)

Murphy, Garth Ivor
J 22(1): 191 (catch equation solution)

Muscle (*see also* Myosin; Protein)
J 22(1): 83 (post-mortem glycolytic changes in Atlantic cod)
(3): 643 (lysolecithinase in Atlantic cod)
(3): 653 (*p*H re halibut flesh chalkiness)
(3): 861 (cause of orange-red colour in scallops)
(4): 929 (oxidative rancidity in lean cod)
(6): 1397 (lateral: effort metabolism of carp)
S 894 (adenine-deaminating enzymes in lingcod)

Muskellunge (*see* Maskinonge)

Mussel, blue (*Mytilus edulis*)
J 22(2): 281 (light effect on growth)
S 891 (water-pumping behaviour recording apparatus)

Mussel, horse (*Vosella modiolus*)
J 22(5): 1137 (low toxicity from *Gonyaulax*)

Mya arenaria (*see* Clam, softshell)

Myctophidae (*see* Lanternfishes)

Myosin and myogens
J 22(1): 203, 215 (electropherograms re fish biochemical systematics)

Mysis relicta (a malacostracan)
J 22(4): 969 (Algonquin Park, Ont., distribution)

Mytilicola orientalis (parasitic copepod)
J 22(4): 1099 (seasonal size distribution re parasitism on Pacific oyster)

Mytilus edulis (*see* Mussel, blue)

Myxocephalus quadricornis (*see* Sculpin, fourhorn)

Myxophyceae
J 22(5): 1107 (lipid fatty acids)

Myxosporidia
J 22(3): 849 (*Henneguya salmonicola* parasitic in Pacific salmons)

N

Nassarius obsoletus (*see* Snail, eastern mud)

Neave, Ferris
S 899 (Pacific salmon)

Nelson, Joseph Schieser
J 22(3): 721 (dams and fish introduction effects on Kananaskis fishes)

Nematoda (hookworms, roundworms)
J 22(6): 1387 (*Dactinis*, etc. re Pacific salmons biological information)

Nets
CPO 1965-7 (comparison of, for zooplankton)
S 928 (catch size effect on otter trawl selectivity)
954 (minimum mesh sizes for different materials, re ICNAF regulations)

Newfoundland area
J 22(1): 237 (skate abnormalities)
(2): 259 (five rare skate species)
(2): 411 (quality of frozen trap cod)
(2): 465 (cod catch, age, size in Bonavista longlining)
(2): 599 (Humber River and Bay of Islands salmon investigations)
(3): 783 (quality of frozen trap cod)
S 893, 905, 965 (salmon and trout investigation and management research programs)
906 (1964 squid fishery prospects)
970 (new cod fishing grounds off NE. coast)

Nickel compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)

Nickerson, Richard Barrett
J 22(1): 101 (king crabs)

Nicol, Joseph Arthur Colin
J 22(2): 513 (flatfishes retinomotor changes)

Nicola Lake, B.C.
J 22(3): 665 (factors affecting kokanee spawning)

Nitrate
B 125R: 73 (determination for sea water)

Nitrite
B 125R: 79 (determination for sea water)

Nitrogen, organic
B 125R: 89, 143 (determination for sea water)

Nomographs
J 22(6): 1575 (for chlorophyll *a*, *b*, *c* phytoplankton pigment spectrophotometry)

Northcote, Thomas Gordon
J 22(3): 665 (movement of mature kokanee)

Northumberland Strait, Gulf of St. Lawrence
J 22(2): 353 (drift-bottle current measurements)

Northwest Territories, Canada (N.W.T.)
J 22(1): 225 (Fury and Hecla Strait currents)
(6): 1571 (fall domestic fishery at Snowdrift, Great Slave Lake)

Nota, Dirk Johannes Gregorius
S 957 (depositional conditions in the St. Lawrence region)

Nucleosides and nucleotides (*see also* Acids, nucleic)
J 22(2): 307 (of pink shrimp)
S 897 (synthesis by steelhead trout milt extract)
914 (synthesis of cyclic phosphates)

Nutrition value (*see also* Feed)
CVG 34 (antioxidant value in protecting herring meal)
S 929 (fish protein concentrate)
969 (antioxidant value in protecting herring meal)

Nymphomyiidae (aquatic flies)
S 963 (new genus found in N.B.)

O

Oceanography, B.C. coast (*see also* Georgia, Strait of; Pacific Ocean; Pollution)
J 22(3): 801 (pollution re water exchange, Port Moody)
(3): 825 (Indian Arm, re ostracod distribution)
(6): 1425 (salinity and tides re intertidal algae distribution)
CPO 1965-2 (mean monthly surface temperatures)
1965-4 (mean monthly surface salinities)
S 918 (daily and seasonal sea-level oscillations)

Oceanography, Canadian Arctic
J 22(1): 225 (Fury and Hecla Strait currents)

Oceanography, Canadian coastal Atlantic (*see also* Hydrography)
J 22(6): 1321 (surface temperatures and heat exchanges re marine climate)
S 888 (ICNAF research report)
953 (Gulf of St. Lawrence marine geology)

Oceanography, general chemical
J 22(1): 113 (seawater Mg ion activity coefficient)
B 125R (seawater analyses manual)

Oceanography, north and northeast Pacific
J 22(3): 689 (first use of transponding buoys)
S 917 (regions and processes in seasonal zone)
919 (insolation re cloud amount and sun altitude)
925, 927 (INPFC Canadian research reports, 1962, 1963)

Odense, Paul Holger
CHN 20 (identification of fillets)

Odours
J 22(4): 875 (in fishery products caused by dimethyl sulphide)
(4): 929 (associated with oxidative rancidity in cod flesh)
(4): 955 (in salmon canned after partial freezing)

Ogilvie, David Malcolm
J 22(2): 503 (DDT on temperature selection)

Oils, marine animal (*see also* Acids, fatty; Antioxidants; Lipids)
J 22(4): 955 (in salmon and trout canned after partial freezing)

Oncorhynchus gorbuscha (*see* Salmon, pink)

Oncorhynchus kisutch (*see* Salmon, coho)

Oncorhynchus nerka (*see* Salmon, sockeye)

Oncorhynchus tshawytscha (*see* Salmon, chinook)

Ontario, Lake (*see* Great Lakes)

Ophiodon elongatus (*see* Lingcod)

Ophiuroidea (*see* Brittlestars)

Osmerus mordax (*see* Smelt, American)

Ostracoda (*see also* common names)
J 22(3): 823 (diurnal and seasonal distribution changes of two *Conchoecia*)

Ostrea edulis (*see* Oyster, European)

Otoliths
J 22(2): 568 (re American plaice age)

Oxygen, dissolved
J 22(1): 159 (mass transfer theory for fish-egg respiration)
(3): 823 (re marine ostracod distribution)
(6): 1491 (consumption re sockeye size and swimming speed)
B 125R: 23 (determination for sea water)
S 892 (re pulp-mill wastes pollution effects)
927 (consumption by lobster)

Oyster, Atlantic (*Crassostrea virginica*)
J 22(2): 281 (light effect on growth)
(2): 631 (ancient shells in now oyster-barren areas)

Oyster, European (*Ostrea edulis*)
S 891 (water-pumping behaviour recording apparatus)

Oyster, Pacific (*Crassostrea gigas*)
J 22(4): 1099 (effect of *Mytilicola* parasite on condition)

P

Pacific Ocean, north (*see also* Oceanography)
S 899 (stocks and fishery developments of salmons)
917 (oceanographic regions and processes in seasonal zone)

Pacific Ocean, northeast (*see also* Oceanography)
J 22(1): 33 (estimating salmon mortality)
(5): 1151 (distribution of two Alepocephalidae)
CPO 1965-2 (B.C. coastal surface temperatures, 1964)
1965-4 (B.C. coastal surface salinities, 1964)
S 918 (daily and seasonal sea-level oscillations, B.C. coast)
925, 926 (salmons research and oceanography)

Pacific Ocean, northwest (*see also* Oceanography)
S 899 (stocks and fishery developments of salmons)

Pagophilus groenlandica (*see* Seal, harp)

Paloheimo, Jyri Erkki
J 22(2): 521 (growth of fishes)

Pancreas
S 967 (triglyceride-hydrolyzing lipase from skate)

Pandalus borealis (*see* Shrimp, pink)

Paralithodes camtschatica (*see* Crab, king)

Parasites and parasitism
J 22(2): 265 (of Jensen's skate)
(3): 849 (myxosporidian, in Pacific salmons)
(4): 1099 (*Mytilicola* seasonal size distribution re parasitism on Pacific oyster)
(4): 1103 (*Anonyx* on lobster)
(5): 1175 (*Piscicola* leech on salmonids)
(6): 1387 (as source of Pacific salmons biological information)
S 925, 926 (aid to distinguishing NE. Pacific salmon stocks)
937 (Trematoda genera review)
948 (Protozoa, in *Limnoria*)
951 (*Caligus gurnardi* copepod review and redescription)

Parker, Robert Ray
J 22(6): 1523 (sea mortality rates for pink salmon)
S 951 (*Caligus gurnardi* Krøyer)

Parophrys vetulus (*see* Sole, lemon (Pacific))

Parsons, Timothy Richard
B 125R (a manual of sea water analysis)
S 923 (determination of plant pigments)
924 (microdetermination of chlorophyll)

Pathological conditions (*see* Disease; Injury)

Pentagramma (Trematoda)
S 937 (review of genus, and *P. petrowi* on B.C. coast fishes)

Perca flavescens (*see* Perch, yellow)

Perch, Pacific Ocean (*see* Rockfish, longjaw)

Perch, yellow (*Perca flavescens*)
B 149: 19, 118 (Great Lakes, catches)

Percopsis omiscomaycus (*see* Trout-perch)

Petromyzon marinus (*see* Lamprey, sea)

Phosphorus compounds (*see also* Phosphates)
B 125R: 43, 141 (determination for sea water)

Phosphates
J 22(1): 53 (poly-, effects on drip loss and rancidity)
(3): 783 (poly-, effects on thaw-drip of cod fillets)
(3): 793 (phosphatase activity in marine phytoplankters)
(4): 929 (re oxidative rancidity in lean cod flesh)
B 125R: 43 (determination for sea water)

Photography
J 22(4): 1025 (time-lapse, of sonar traces of migrating smolts)

Photoperiods (*see* Light, reactions to)

Photosynthesis
J 22(4): 1083 (re marine phytoplankton carbon balance)
B 125R: 165 (rate measurement in sea water)

Phytoplankton
J 22(3): 793 (phosphatase activity of some marine)
(4): 1083 (carbon balance of marine)
(5): 1107 (lipid fatty acids of marine)
(6): 1575 (nomographs for chlorophyll *a*, *b*, *c* spectrophotometry)
B 125R: 117 (pigment determination for sea water)
S 908 (of Canadian large lakes)

Pickerel (*see* Pike, northern; *also* Walleye)

Pickerel, blue (*see* Pike, blue)

Pickerel, chain (*Esox niger*)
J 22(5): 1261 (hybrids with other Esocidae)

Pickerel, grass (*Esox americanus vermiculatus*)
J 22(5): 1261 (hybrids with other Esocidae)

Pickerel, redfin (*Esox americanus americanus*)
J 22(5): 1261 (hybrids with other Esocidae)

Pickerel, yellow (*see* Walleye)

Pigments and pigmentation
J 22(3): 861 (zeaxanthin cause of scallop orange-red meats)
(4): 955 (re quality of canned partially frozen salmon)
(6): 1575 (nomographs for phytoplankton chlorophyll *a*, *b*, *c*, spectrophotometry)
B 125R: 117 (determination of phytoplankton, in sea water)
CHN 22 (by sulphur compounds in canned products)
S 923, 924 (spectrophotometric determination of marine-plant)

Pike, blue (*Stizostedion vitreum glaucum*) (blue walleye; blue pickerel)
B 149: 19, 118 (Great Lakes, catches)

Pike, northern (*Esox lucius*) (pickerel; jackfish)
J 22(3): 744 (in Bow River system, Alta.)
(5): 1261 (hybrids with other Esocidae)
(6): 1357 (feed of, in Heming Lake, Man.)
B 149: 19, 120 (Great Lakes, catches)

Pike, yellow (*see* Walleye)

Pikeperch, yellow (*see* Walleye)

Pimephales promelas (*see* Minnow, flathead)

Pinhorn, Allenby Thomas
J 22(2): 369 (*Salmo salar* behavior)

Piscicola salmositica (*see* Leech, salmonid)

Pitt, Thomas Kenton
J 22(1): 247 (modified whirling vessel)

Pituitary glands
S 962 (salmon hormones effect on immature trout gonads)

Placopecten magellanicus (*see* Scallop, giant)

Plaice, American (*Hippoglossoides platessoides*)
J 22(2): 565 (life history, ecology, in Magdalen Shallows)
(6): 1345 (lymphocystis disease on eastern Grand Bank)
S 886, 887, 949, 955 (ICNAF research reports)

Plaice, European (*Pleuronectes platessa*)
J 22(2): 513 (retinomotor changes)

Plankton (*see also* Phytoplankton; Zooplankton)
CPO 1965-3, 5, 7, 8 (observations in Strait of Georgia)
S 956 (Caribbean Sea Canadian research)

Plasma, blood
J 22(3): 767 (electropherograms re salmonids and their hybrids for biochemical systematics)
(6): 1455 (composition re goldfish thermal acclimation)

Platford, Robert Frederick
J 22(1): 113 (magnesium ion in sea water)
(4): 885 (sodium ion in sea water)

Platichthys stellatus (*see* Flounder, starry)

Plecoptera (*see* Stoneflies)

Pleuronectes platessa (*see* Plaice, European)

Pleuronichthys coenosus (*see* Sole, C-O)

Poacher, sturgeon (*Agonus acipenserinus*)
J 22(1): 203 (biochemical systematics)

Poisons (*see* Insecticides; Pollution; Toxicity)

Pollachius virens (*see* Pollock)

Pollock (*Pollachius virens*)
J 22(6): 1555 (swimbladder volume determination method)
S 887, 955 (ICNAF research reports)

Pollution (*see also* Radioactivity)
J 22(2): 425 (Cu–Zn solutions toxicity to young Atlantic salmon)
(3): 801 (disposal re water exchange, Port Moody, B.C.)
S 892, 907, 959 (problems of pulp-mill wastes disposal)
931, 961 (Cu–Zn solutions toxicity to young Atlantic salmon)
960 (apparatus for studying avoidance by young Atlantic salmon)
964 (mathematical analysis of multivariable environments effects)

Polyipnus asteroides (*see* Hatchetfish)

Polyphosphates (*see* Phosphates)

Pontoporeia affinis (a malacostracan)
J 22(4): 969 (Algonquin Park, Ont., distribution)

Populations
J 22(2): 395 (brook trout re stream siltiness)
(5): 1197 (year-class fluctuations of Lake Erie whitefish)
(5): 1229 (growth and morphology of pygmy whitefish)
S 902 (management for Canadian fisheries development)

Port Moody, B.C.
J 22(3): 801 (water exchange re pollution disposal)

Potassium compounds
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)

(4): 955 (K ion decrease in salmon held in refrigerated sea water)
(6): 1455 (in goldfish blood plasma)
S 947 (K ion changes in fish held in refrigerated sea water)
957 (in St. Lawrence River and Gulf sediments)

Powell, Guy Charles
J 22(1): 101 (king crabs)

Power, Henry Edwin
CHN 21 (lobster display unit)
S 929 (fish protein concentrate)

Powles, Percival Mount
J 22(2): 565 (Magdalen Shallows plaice)
(6): 1565 (new size record for greysole)

Prakash, Anand
S 916 ("red water" phenomenon)

Predation
J 22(2): 577 (cod on American plaice)

Preservatives and preservative treatments (*see also* Antibiotics; Antioxidants; Freezing; Rancidity; Refrigeration)
J 22(1): 53 (polyphosphates, citrate, and salt against drip loss and rancidity)
S 889 (against bacterial fish spoilage)

Prickleback, longsnout (*Lumpenella longirostris*)
J 22(1): 203 (biochemical systematics)

Prickleback, snake (*Lumpenus sagitta*)
J 22(1): 203 (biochemical systematics)

Prince Edward Island (*see* Bideford River; Ellerslie Brook; Northumberland Strait)

Pritchard, Andrew Lyle
S 902 (population management)

Processing (*see also* individual types of processing)
B 149: 53 (of Great Lakes fisheries)
S 904 (Canadian research on)

Products (*see also* individual types of products; *also* under names of certain fishes)
B 149: 53 (of Great Lakes fisheries)
S 904 (Canadian research on)

Pro-oxidants (*see* Rancidity)

Prosopium coulteri (*see* Whitefish, pygmy)

Prosopium cylindraceum (*P. quadrilaterale*) (*see* Whitefish, round)

Prosopium williamsoni (*see* Whitefish, mountain)

Protein (*see also* Muscle; Protein concentrate)
J 22(1): 13 (salting and smoking effects on quality of cod)
(3): 653 (denaturation re halibut flesh chalkiness)
(4): 955 (proteolysis in canning of feedy salmon)
B 125R: 161 (determination for sea water)
CVG 34 (value of herring meal)
S 969 (value of herring meal)

Protein concentrate ("fish flour")
S 929 (processing and characteristics)

Psettichthys melanostictus (*see* Sole, sand)

Pseudopleuronectes americanus (*see* Flounder, winter)

Pterolamiops longimanus (*see* Whitetip)

Pulpmills
S 892, 907, 959 (wastes disposal problems)

Pumpkinseed (*Lepomis gibbosus*)
J 22(2): 405 (respiratory metabolism re swimming speed)

Pycha, Richard Lawrence
J 22(4): 999 (movement of trout in Lake Superior)

Pyrrophyta
J 22(4): 1083 (carbon balance)

Q

Quahaug (*Mercenaria mercenaria*)
J 22(2): 281 (light effect on growth)
(2): 631 (ancient shells in now quahaug-barren areas)

Quality of products; quality assessment (*see also* Antibiotics; Antioxidants; Preservatives)
J 22(1): 13 (smoked and salted cod protein)
(1): 17, 27 (carbonyl compounds re salted cod flavour)
(1): 53 (drip loss and rancidity inhibitors for frozen salmon)
(1): 83 (glycolytic changes in cod muscle)
(2): 411 (re freezing rate and frozen stored trap cod)
(3): 783 (thaw-drip of untreated vs. polyphosphate-treated fillets)
(3): 861 (orange-red-pigmented scallop meats)
(3): 865 (re tapeworm cysts in lake whitefish fillets)
(4): 955 (canned partially frozen Pacific salmons)
(5): 1131 (*Limacina* feed affecting B.C. groundfish)
S 889 (preventing bacterial spoilage of fish)
904 (Canadian research on)

Quayle, Daniel Branch
S 948 (marine wood borers)

R

Radioactivity
S 941 (pollution re B.C. coast marine environment and fisheries)

Raja erinacea (*see* Skate, little)

Raja fyllae (an Atlantic deep-water skate)
J 22(4): 910 (denticles re identification aid)

Raja hyperborea (*see* Skate, arctic)

Raja jenseni (*see* Skate, Jensen's)

Raja laevis (*see* Skate, barndoor)

Raja lintea (a skate)
J 22(2): 265 (Nfld. distribution and scarcity)

Raja mollis (a skate)
J 22(2): 268 (Nfld. distribution and scarcity)

Raja ocellata (*see* Skate, winter)

Raja radiata (*see* Skate, thorny)

Raja senta (*see* Skate, smooth)

Raja spinacauda (*see* Skate, spinytail)

Rake
S 909 (hydraulic, for softshell clam harvesting)

Ramsay, Barbara Ann
J 22(2): 425 (toxicity of metal salts mixtures to salmon)

Rancidity, oxidative (*see also* Antioxidant)
J 22(4): 955 (development in salmon held in refrigerated sea water)

Range, extension of
J 22(1): 231 (four rockfishes in N. Pacific)
(4): 977 (many NW. Atlantic Mollusca)
(5): 1303 (hatchetfish in W. Atlantic)
(5): 1305 (dusky sculpin into B.C. waters)
(6): 1559 (window rockfish into B.C. coast)

Ratfish (*Hydrolagus colliei*)
J 22(1): 203 (biochemical systematics)

"Red tide"
J 22(4): 1083 (carbon balance of causative dinoflagellates)

"Red water"
S 916 (occurrence on west coast of India)

Redfish (*Sebastes marinus* and *S. mentella*)
S 886, 890, 928, 930, 949, 955 (ICNAF research reports)
928 (catch size effect on otter trawl selectivity)

Refrigerated sea water (*see* Sea water, refrigerated)

Refrigeration
J 22(2): 411 (re freezing rate and quality of frozen trap cod)

Renshaw, Roby Ward
J 22(3): 841 (*Calycopsis nematophora* distribution)

Reproduction (*see also* Eggs)
J 22(1): 101 (king crabs)
(2): 448 (harp seals)

Respiration, and metabolism of
J 22(1): 159 (oxygen mass transfer theory for fish eggs)
(2): 405 (re pumpkinseed swimming speed)
(6): 1491 (re sockeye swimming speed and size)
S 896 (young sockeye swimming energy requirements)
927 (lobster oxygen consumption)

Retina (*see* Eye)

Rhinichthys atronasus (= *atratulus*) (*see* Dace, blacknose)

Rhinichthys cataractae (*see* Dace, longnose)

Rhode Island, U.S.A.
J 22(4): 945 (estimating theoretical biomass of young winter flounder for a fishery)

Ribonucleic acid (*see* Acids, nucleic)

Richards, Sarah Wheatland
J 22(5): 1313 (postlarvae of the sand lance)

Ricker, William Edwin
J 22(2): 475 (stoneflies)
(6): 1477 (salmon scale annuli)
S 900 (availability of fish)
968 (distribution of Canadian stoneflies)

Rigor
S 947 (re ionic concentration changes in muscle)

Roach, Stewart Williard
J 22(4): 955 (partial freezing of salmon)

Roberts, Eve
J 22(1): 203 (muscle myogens of vertebrates)
(1): 215 (*Oncorhynchus* species identification)
(3): 767 (salmonid hybrids)

Roccus chrysops (*see* Bass, white)

Rockfish, copper (*Sebastodes caurinus*)
J 22(1): 203 (biochemical systematics)

Rockfish, dusky (*Sebastodes ciliatus*)
J 22(1): 203 (biochemical systematics)

Rockfish, flag (*Sebastodes rubrivinctus*)
J 22(1): 231 (N. Pacific range extension)

Rockfish, greenstripe (*Sebastodes elongatus*)
J 22(1): 203 (biochemical systematics)

Rockfish, longjaw (*Sebastodes alutus*) (Pacific ocean perch)
J 22(1): 203 (biochemical systematics)
(5): 1309 (rapid length distribution measurement)

Rockfish, northern (*Sebastodes polyspinus*)
J 22(1): 203 (biochemical systematics)

Rockfish, quillback (*Sebastodes maliger*)
J 22(1): 203 (biochemical systematics)

Rockfish, rosethorn (*Sebastodes helvomaculatus*)
J 22(1): 231 (N. Pacific range extension)

Rockfish, rougheye (*Sebastodes aleutianus*)
J 22(1): 203 (biochemical systematics)

Rockfish, sharpchin (*Sebastodes zacentrus*)
J 22(1): 231 (N. Pacific range extension)

Rockfish, spinycheek (*Sebastolobus alascanus*)
J 22(1): 203 (biochemical systematics)

Rockfish, widow (*Sebastodes entomelas*)
J 22(6): 1559 (new to B.C. coast)

Rockfish, yellowtail (*Sebastodes flavidus*)
J 22(1): 203 (biochemical systematics)

Rodriguez, Jorge Luis
J 22(3): 869 (haematology of hake)

Roelofs, Eugene Woodrow
J 22(6): 1379 (photoperiod effects on sunfish)

Ronald, Keith
J 22(5): 1299 (blood clotting in cod)
S 898 (blood of aquatic vertebrates)

Ronquil (*Bathymaster leurolepis*)
J 22(5): 1293 (new species, and key to *Bathymaster*)

Ross, Avron John
J 22(3): 713 (redmouth disease)

Rushton, Donald Kenneth
S 911 (barachois ponds)

S

Sablefish (*Anoplopoma fimbria*)
J 22(1): 203 (biochemical systematics)

Saila, Saul Bernhard
J 22(4): 945 (juvenile winter flounder)

Salinity
J 22(1): 239 (deep water of Baker Lake, N.W.T.)
(3): 823 (re ostracod distribution, Indian Arm, B.C.)
(6): 1425 (re intertidal algae distribution)
B 125R: 11 (determination for sea water)
CPO 1965-1 (salinometers modifications)
1965-4 (monthly mean surface, at B.C. coastal stations)

Salmo clarki lewisi (*see* Trout, Yellowstone cutthroat)

Salmo clarki (see Trout, cutthroat)

Salmo gairdneri (*see* Trout, steelhead; Trout, rainbow)

Salmo salar (*see* Salmon, Atlantic)

Salmo trutta (*see* Trout, brown)

Salmon, Atlantic (biology) (*Salmo salar*)
J 22(2): 335 (swimbladder size re buoyancy of parr and smolts)
(2): 369 (behaviour of young in light gradients)
(2): 421 (toggle tag new design)
(2): 425 (Cu–Zn solutions lethal levels for young)
(2): 503 (DDT effect on temperature selection by young)
(2): 599 (Humber River and Bay of Islands, Nfld. investigations)
(2): 625 (Canadian tagged recovery near Greenland)
(3): 732 (unsuccessful transplant into Kananaskis River, Alta.)
(6): 1567 (precocious sexual development in laboratory-reared male)
S 893, 905, 965 (investigation and management research program, 1962–63; 1963–64; 1961–62)
920 (forest spraying re angling)
931 (avoidance of Cu–Zn solutions)
960 (apparatus for studying pollutant avoidance by young)
961 (Zn and Cu effects on migration)

Salmon, chinook (biology) (*Oncorhynchus tshawytscha*) (*see also* Salmons, Pacific)
J 22(1): 167 (mass transfer theory for egg respiration)
(3): 849 (myxosporidian parasite)
S 962 (pituitary hormones effect on immature trout gonads)

Salmon, chinook (products)
J 22(1): 53 (drip and rancidity inhibitors)

Salmon, chum (biology) (*Oncorhynchus keta*) (*see also* Salmons, Pacific)
J 22(4): 919 (stream sediment rate effects on)
(6): 1477 (supplementary checks on scales)

Salmon, coho (biology) (*Oncorhynchus kisutch*) (*see also* Salmons, Pacific)
J 22(1): 173 (environmental and behavioural ecology of juvenile)
(3): 849 (myxosporidian parasite)

(4): 1035 (behaviour, ecology, interaction, re young steelhead)
CPO 1965-6 (NW. Strait of Georgia commercial troll catches)
S 962 (pituitary hormones effect on immature trout gonads)
964 (mathematical treatment of toxic environment effect on young)

Salmon, coho (products)
J 22(4): 955 (canning after holding partially frozen)

Salmon, masu (*see* Masu)

Salmon, pink (biology) (*Oncorhynchus gorbuscha*) (*see also* Salmons, Pacific)
J 22(3): 849 (myxosporidian parasite)
(4): 919 (stream sedimentation rate effects on)
(6): 1477 (supplementary checks on scales)
(6): 1523 (sea mortality rate estimation)
S 937 (parasitism by *Pentagramma petrowi* trematode)
951 (parasitism by *Caligus gurnardi* copepod)
952 (migration, composition, exploitation, abundance, of odd-year Fraser River run)

Salmon, sockeye (biology) (*Oncorhynchus nerka*) (*see also* Kokanee; Salmons, Pacific)
J 22(1): 33 (estimating ocean mortality; applications)
(3): 755 (histology of post-spawning death after maturing and spawning in captivity)
(4): 891 (acetone bodies in blood of starved pre-spawning)
(4): 1025 (recording smolt movements by time-lapse photography of sonar traces)
(6): 1491 (size re swimming speed and O_2 consumption)
(6): 1503 (egg and sperm holding time re fertility)
S 896 (swimming energy of young)
937 (parasitism by *Pentagramma petrowi* trematode)
962 (pituitary hormones effect on immature trout gonads)

Salmon, sockeye (products)
J 22(4): 955 (canning after holding partially frozen)
S 947 (Na, K, Mg ion concentration and weight changes re rigor)

Salmon, steelhead (*see* Trout, steelhead)

Salmons, Pacific (biology) (inclusive; *see also* individual species)
J 22(1): 203, 215 (biochemical systematics and speciation)
(5): 1175 (*Piscicola* freshwater leech parasitism)
(6): 1387 (parasites as information source re biology of)
(6): 1563 (degradative digestive rate of feed)
S 899 (ocean stocks and fishery development)
925, 926 (INPFC Canadian research reports, 1962, 1963)
934 (angiography; radiography of cardiovascular system)

Salt, common
J 22(1): 53 (retards drip loss; accelerates rancidity)
(4): 929 (rancidity promoter in lean cod muscle)

Salting and salted products
J 22(1): 13 (salting effects on cod protein quality)
(1): 17, 27 (carbonyl compounds re flavour of cod)

Salts, metal (*see also* Salt, common; *also* names of elements)
J 22(4): 929 (re oxidative rancidity promotion in cod flesh)

Salvelinus alpinus (*see* Char, Arctic)

Salvelinus alpinus willughbii (*see* Char, Windermere)

Salvelinus fontinalis (*see* Trout, brook)

Salvelinus malma (*see* Dolly Varden)

Salvelinus namaycush (*see* Trout, lake)

Sandfish (*Trichodon trichodon*)
J 22(1): 203 (biochemical systematics)

Sandlances (*Ammodytes* species)
J 22(5): 1313 (description of postlarval stages from W. Atlantic)

Sarda lineolata (*see* Bonito, Pacific)

Sarma, Anchal Harish Viswanatha
S 916 ("red water" phenomenon)

Sauger (*Stizostedion canadense*)
B 149: 19, 122 (Great Lakes, catches)

Saunders, John Wilfred
J 22(2): 395 (brook trout population)

Saunders, Richard Lee
J 22(2): 335 (swimbladder of Atlantic salmon)
(2): 625 (Canadian salmon off Greenland)
(6): 1567 (Atlantic salmon development)

Scales
J 22(6): 1477 (supplementary checks on, in salmons)

Scallop, giant (*Placopecten magellanicus*) (sea scallop)

J 22(2): 313 (comparative catches by dragring size)
(3): 861 (orange-red meat due to zeaxanthin pigment)
(5): 1137 (paralytic poison from *Gonyaulax*)
S 887, 955 (ICNAF research reports)
910 (natural and fishing mortality causes)

Scarratt, David Johnson
J 22(2): 421 (new toggle tag)
(4): 1103 (predation on lobsters by *Anonyx*)

Schmidt, Peter Joseph
S 962 (pituitary hormones of salmon)

Scorpaenichthys marmoratus (*see* Cabezon)

Scott, William Beverley
J 22(5): 1303 (hatchetfish range extension)

Sculpin, dusky (*Icelinus burchami*)
J 22(5): 1305 (first B.C. record)

Sculpin, fourhorn (*Myoxocephalus quadricornis*)
J 22(4): 969 (Algonquin Park, Ont., distribution)

Sea level
S 918 (daily and seasonal oscillations, B.C. coast)

Sea water
J 22(5): 1107 (fatty acids in dissolved and particulate matter)
B 125R (manual for analysis)
S 912 (system and pumps for large aquarium tanks)

Sea water, refrigerated (for holding fishery products)
J 22(4): 955 (normal and salt-fortified, for salmon before canning)
S 935 (for chilling fish on board vessels)
947 (Na, K, Mg ion concentration in muscle after holding fish in)

Seal, grey (*Halichoerus grypus*)
S 932 (lactating female blubber fatty acid composition)

Seal, harp (*Pagophilus groenlandica*)
J 22(2): 433 (NW. Atlantic migrations)
S 938 (NW. Atlantic industry)

Seal, hooded (*Cystophora cristata*)
S 938 (NW. Atlantic industry)

Seaperch, shiner (*Cymatogaster aggregata*)
J 22(1): 203 (biochemical systematics)

Seaweeds
J 22(6): 1425 (distribution of intertidal re salinity and tides)

Sebastodes aleutianus (*see* Rockfish, rougheye)

Sebastodes alutus (*see* Rockfish, longjaw)

Sebastodes caurinus (*see* Rockfish, copper)

Sebastodes ciliatus (see Rockfish, dusky)

Sebastodes elongatus (*see* Rockfish, greenstripe)

Sebastodes entomelas (*see* Rockfish, widow)

Sebastodes flavidus (*see* Rockfish, yellowtail)

Sebastodes goodei (*see* Chilipepper)

Sebastodes helvomaculatus (*see* Rockfish, rosethorn)

Sebastodes maliger (*see* Rockfish, quillback)

Sebastodes polyspinus (*see* Rockfish, northern)

Sebastodes ruberrimus (*see* Snapper, red)

Sebastodes rubrivinctus (*see* Rockfish, flag)

Sebastodes zacentrus (*see* Rockfish, sharpchin)

Sebastolobus alascanus (*see* Rockfish, spinycheek)

Sedimentation (*see also* Silt)
J 22(3): 801 (re water exchange and pollution in an inlet)
(4): 919 (rate in Alaskan salmon stream)
S 957 (St. Lawrence River and Gulf recent depositional conditions)
959 (mathematical treatment of, for pulpmill effluents)

Selectivity of gear (*see* Nets; Trawl)

Senecella calanoides (a copepod)
J 22(4): 969 (Algonquin Park, Ont., distribution)

Sergeant, David Ernest
J 22(2): 433 (harp seal migrations)
S 938 (sealing industry)

Seriola dumerili (see Amberjack, greater)

Serum, blood
S 943 (effect on rainbow trout gonadal cell growth)

Sex ratio
J 22(3): 681 (Nicola Lake, B.C., kokanee)
(3): 695 (and sexual dimorphism, immature sea lampreys)

Shapley, Sanford Philip
J 22(4): 919 (sediment in streams)

Shark, dusky (*Carcharhinus obscurus*)
S 956 (Canadian research in Caribbean Sea)

Shark, sandbar (*Carcharhinus milberti*)
S 956 (Canadian research in Caribbean Sea)

Shark, sickle (*Carcharhinus falciformis*)
S 956 (Canadian research in Carribbean Sea)

Shark, sixgill (*Hexanchus griseus*) (*H. corinus*)
J 22(3): 857 (description and morphometry, San Juan Islands specimen)

Shark, tiger (*Galeocerdo cuvieri*)
S 956 (Canadian research in Caribbean Sea)

Sheepshead (*see* Drum, freshwater)

Shell
J 22(2): 281 (growth and structure, Atlantic Oyster, mussel, quahaug)
(2): 631 (ancient oyster and quahaug in now-barren areas)
(3): 851 (Mn deposits on mud snail, P.E.I.)
S 910 (damage repairability of sea scallop)

Shellfish (*see also* common names of species)
S 900 (availability of Canadian)

Shellfish toxicity
J 22(5): 1137 (in Atlantic scallop organs, from *Gonyaulax*)
S 916 (re "red water" on west coast of India)

Shieh, Hang-shan
S 933 (degradation of choline)
936 (degradation of choline)

Shinners, Claude Wayne
CHN 20 (identification of fillets)

Shipworms (*see also* Gribbles)
S 948 (*Bankia* and *Teredo* in B.C. coastal waters)

Shrimp, pink (*Pandalus borealis*)
J 22(2): 307 (nucleotides, sugars, homarine)

Shrimps (Pacific) (*see also* individual species)
J 22(1): 117 (antibiotic preservation)

Silica and silicates
B 125R: 67 (determination for sea water)
S 957 (in St. Lawrence River and Gulf sediments)

Silt (*see also* Sedimentation)
J 22(2): 395 (effect on brook trout stream population)

Sipos, John Charles
S 921 (response of fatty acids and esters in gas chromatography)

Size
J 22(2): 465 (trends in Nfld. longlined cod)
(2): 573 (mature American plaice)
(2): 605 (re age composition of Nfld. salmon)
(3): 679 (Nicola Lake, B.C., kokanee)
(4): 1083 (seasonal distribution of *Mytilicola*, re parasitism on Pacific oyster)
(6): 1372 (of northern pike re size of feed)
(6): 1491 (of sockeye re swimming speed and O_2 consumption)
(6): 1565 (new record for witch flounder)
S 908 (to depth relation of lakes)

Skate (a Pacific species)
J 22(1): 203 (biochemical systematics)

Skate, Arctic (*Raja hyperborea*)
J 22(2): 262 (Nfld. distribution and scarcity)

Skate, barndoor (*Raja laevis*)
J 22(1): 237 (snout abnormality)
(4): 910 (denticles re identification aid)
S 967 (triglyceride-hydrolyzing lipase from pancreas)

Skate, Jensen's (*Raja jenseni*)
J 22(2): 264 (Nfld. distribution and scarcity)
(4): 910 (denticles re identification aid)

Skate, little (*Raja erinacea*)
J 22(2): 260 (Nfld. distribution and scarcity)
(4): 899 (distinguishing from winter skate)

Skate, smooth (*Raja senta*)
J 22(4): 910 (denticles re identification aid)

Skate, spinytail (*Raja spinacauda*)
J 22(4): 910 (denticles re identification aid)

Skate, thorny (*Raja radiata*)
J 22(1): 237 (various abnormalities)
(4): 910 (denticles re identification aid)

Skate, winter (*Raja ocellata*)
J 22(4): 899 (distinguishing from little skate)

Skin
J 22(6): 1345 (lymphocystis disease of American plaice)
S 938 (NW. Atlantic seal industry)

Slavin, Joseph William
S 935 (chilling and freezing on board vessels)

Sloan, Phillip Reid
J 22(4): 1083 (phytoplankton photosynthesis)

Smart, Michael John
S 934 (*in vivo* angiography)

Smelt, American (*Osmerus mordax*)
B 149: 20, 122 (Great Lakes, catches)

Smelt, longfin (*Spirinchus dilatus*)
S 937 (*Pentagramma petrowi* trematode parasitism)

Smelt, silver (*see* Smelt, surf)

Smelt, surf (*Hypomesus pretiosus*) (silver smelt)
S 937: 394 (*Pentagramma petrowi* trematode parasitism)

Smith, George Francis Maurice
S 900 (availability of fish)
901 (exploration for fisheries resources)
902 (fish population management)

Smith, Michael
J 22(3): 775 (post-spawning death of salmon)
S 895 (deoxyribonucleic acids of Crustacea)
914 (deoxyribonucleoside phosphate synthesis)
962 (pituitary hormones of salmon)

Smith, Morden Whitney
J 22(2): 395 (brook trout population)
S 911 (barachois ponds)

Smoking and smoked products
J 22(1): 13 (smoking effects on cod protein quality)

"Smut"
CHN 22 (nature and control in canned products)

Snail (marine) (*Limacina helicina*)
J 22(5): 1311 (in feed of B.C. groundfish affects quality)

Snail, eastern mud (*Nassarius obsoletus*)
J 22(3): 851 (Mn deposits on shells, P.E.I.)

Snapper, rasphead (*see* Snapper, red)

Snapper, red (*Sebastodes ruberrimus*)
J 22(1): 53 (drip and rancidity inhibitors)

Snappers (*Lutjanus* species)
S 956 (Canadian research in Caribbean Sea)

Snout
J 22(1): 237 (abnormality in barndoor skate)

Snowdrift, N.W.T.
J 22(6): 1571 (fall domestic fishery)

Sodium compounds (*see also* Salt)
J 22(4): 885 (Na ion activity coefficient in sea water)
(4): 929 (re oxidative rancidity promoion in cod flesh)
(4): 955 (Na ion increase in salmon held in refrigerated sea water)
(6): 1455 (in goldfish blood plasma)
S 947 (Na ion changes in fish held in refrigerated sea water)
957 (in St. Lawrence River and Gulf sediments)

Solarolo, E.B.
J 22(1): 243 (acid-fast bacteria)

Sole, butter (*Isopsetta isolepis*)
J 22(1): 203 (biochemical systematics)

Sole, C-O (*Pleuronichthys coenosus*)
J 22(1): 203 (biochemical systematics)

Sole, common (*Solea solea*)
J 22(2): 513 (retinomotor changes)

Sole, Dover (*Miscrostomus pacificus*)
J 22(1): 53 (drip and rancidity inhibitors)
(1): 203 (biochemical systematics)

Sole, flathead (*Hippoglossoides elassodon*)
J 22(1): 203 (biochemical systematics)

Sole, lemon (Pacific) (*Parophrys vetulus*)
J 22(1): 203 (biochemical systematics)
(3): 755 (browning of freeze-dried flesh)

Sole, merry (*Microstomus kitt*)
J 22(2): 513 (retinomotor changes)

Sole, petrale (*see* Brill, Pacific)

Sole, rex (*Glyptocephalus zachirus*)
J 22(1): 203 (biochemical systematics)

Sole, rock (*Lepidopsetta bilineata*)
J 22(1): 203 (biochemical systematics)
(5): 1311 (catch contaminated by pelagic snail)

Sole, sand (*Psettichthys melanostictus*)
J 22(1): 203 (biochemical systematics)

Solea solea (*see* Sole, common)

Sounding, echo
J 22(4): 1025 (time-lapse photography of, for tracing migrating smolt movements)

Southcott, Burnett Anne
J 22(1): 53 (drip loss of frozen fish)
(1): 117 (tetracycline antibiotics)

Sparks, Albert Kirk
J 22(4): 1099 (*Mytilicola orientalis*)

Spawning (*see also* Life history, etc.)
J 22(2): 574 (Magdalen Shallows American plaice)
(3): 775 (histology after death of post-spawning sockeye)
(3): 665 (factors affecting kokanee migration)

Speciation (*see also* Systematics; Taxonomy)
J 22(1): 203, 215 (by electropherograms of myogen and hemoglobin)
(3): 767 (by electropherograms of myogen, plasma, protein)
(4): 899 (distinguishing little from winter skate)
(5): 1293 (distinction between *Bathymaster* ronquils)

Species, introduced or transplanted
J 22(3): 721 (into Kananaskis and Bow Rivers systems, Alta.)
S 948 (*Limnoria punctata* wood borer to B.C. coastal waters)

Species, new
J 22(1): 1 (decapod *Calocaris templemani*)
(1): 139 (lamprey *Lampetra richardsoni*)
(2): 475 (various Plecoptera stoneflies)
(5): 1293 (ronquil *Bathymaster leurolepis*)

S 933, 936 (choline-fermenting *Achromobacter cholinophagum*)
963 (and genus of Nymphomyiidae found in N.B.)

Species, relict
J 22(4): 969 (Crustacea and fish in Algonquin Park, Ont.)

Spermatozoa (*see* Milt)

Sphyraena barracuda (see Barracuda, great)

Sphyrion lumpi (parasitic crustacean)
J 22(2): 421 (head shape inspiration for fish tag shape)

Sphyrna lewini (*see* Hammerhead, scalloped)

Spirinchus dilatus (*see* Smelt, longfin)

Spoilage (*see also* Preservatives; Quality)
S 889 (control in fish products)

Sport fishing (*see also* Angling; Salmon; Trout)
B 149: 107 (Great Lakes)

Sprague, John Booty
J 22(2): 425 (toxicity of metal salt mixtures to salmon)
S 913 (alkaline contamination of tank water supply)
931 (avoidance reactions of fish)
960 (apparatus for studying pollutants avoidance)
961 (determination of safe levels of toxicants)

Squalus suckleyi (see Dogfish, Pacific)

Squid, Newfoundland (*Illex illecebrosus*)
J 22(1): 131 (lipids and component fatty acids)
S 906 (1964 fishery prospects)

Squires, Hubert Jacob
J 22(1): 1 (new species of *Calocaris*)
(1): 69 (larvae of *Argis dentata*)

St. Clair, Lake (*see* Great Lakes)

St. Lawrence, Gulf of (*see also* Belle Isle, Strait of; Northumberland Strait)
J 22(2): 433 (harp seal migration)
CSG 44 (distribution of cod catches)
S 950 (water temperatures re herring fishery)
953 (marine geology)
957 (and St. Lawrence River: recent depositional conditions)

Stanley-Jones, Arthur Roland
CPO 1965-1 (modifications to salinometers)

Stephens, Kenneth
J 22(6): 1563 (degradation of consumed organisms)
(6): 1575 (phytoplankton pigment nomographs)
CPO 1965-1 (modifications to salinometers)

Stewart, James Edward
CHN 21 (lobster display unit)
S 898 (blood of aquatic vertebrates)
943 (growth of rainbow trout)

Stickleback, brook (*Culea* (= *Eucalia*) *inconstans*)
J 22(3): 744 (in Kananaskis River system, Alta.)

Stizostedion canadense (*see* Sauger)

Stizostedion vitreum glaucum (*see* Pike, blue)

Stizostedion vitreum vitreum (*see* Walleye)

Stocking
J 22(2): 721 (past, in Kananaskis River system, Alta.)

Stocks
J 22(2): 591 (delineation for American plaice, Magdalen Shallows)
(4): 945 (estimating theoretical biomass for a winter flounder fishery)
S 899, 925, 926 (ocean, of Pacific salmons, and fishery developments)

Stomach
J 22(3): 775 (histology, of post-spawned sockeye)

Stoneflies
J 22(2): 475 (new records and descriptions of new species)
S 966 (effect of DDT forest spraying in N.B.)
968 (Canadian distribution)

Strickland, John Douglas Hipwell
B 125R (manual of sea water analysis)
S 923 (determination of plant pigments)

Strontium compounds
S 941 (radioactive Sr^{90} seawater contaminant)

Sturgeon, lake (*Acipenser fulvescens*)
B 149: 20, 120 (Great Lakes, catches)

Sucker, longnose (*Catostomus catostomus*)
J 22(3): 740 (in Kananaskis River system, Alta.)

Sucker, white (*Catostomus commersoni*)
J 22(1): 219 (fin anomalies, Heming Lake, Man.)
(3): 742 (in Kananaskis River system, Alta.)

Suckers
B 149: 23, 123 (Great Lakes, catches)

Sugars (*see also* Carbohydrates; Glycogen)
J 22(2): 307 (of pink shrimp)
(3): 755 (ribose and glucose re browning of fish flesh)

Sulphur compounds
J 22(4): 875 (apparatus for detecting dimethyl sulphide precursor in fishery products)
CHN 22 (cause of "smut" in canned products)

Sunfish, green (*Lepomis cyanellus*)
J 22(6): 1379 (photoperiod influence on growth)

Superior, Lake (*see also* Great Lakes)
J 22(4): 999 (movements of hatchery-reared lake trout)

Survival
J 22(2): 385 (lobsters out of water)
(4): 919 (stream sedimentation rate effect on young salmon)

Sutherland, Donald Bain
J 22(2): 405 (pumpkinseed respiration)

Swift, Donald Robert
J 22(4): 913 (char egg development and mortality)

Swimbladder
J 22(2): 335 (volume re young Atlantic salmon and trout buoyancy)
(6): 1555 (volume determination method)

Swimming
J 22(2): 405 (speed re pumpkinseed respiratory metabolism)
(2): 523 (effort re growth and feed)
(6): 1491 (speed of sockeye re size and O_2 consumption)
S 896 (energy of young sockeye compared with drag force of dead fish)

Swordfish (*Xiphias gladius*)
S 956 (Canadian research in Caribbean Sea)

Systematics (*see also* Speciation; Taxonomy)
J 22(1): 203, 215 (biochemical applications to fishes)
(2): 475 (stoneflies)
(3): 767 (biochemical applications to salmonids and their hybrids)

T

Tabata, Susumu
S 919 (insolation and cloud amount)

Tagging methods, returns, and interpretation
J 22(2): 421 ("sphyrion" type tag for fish)
(2): 435 (four tag types for harp seals)
(2): 585 (American plaice, Magdalen Shallows)
(2): 625 (Canadian Atlantic salmon recapture near Greenland)
S 925, 926 (NE. Pacific salmons)

Tail
J 22(1): 237 (abnormalities in thorny skate)

Talismania bifurcata (a deep-water fish)
J 22(5): 1151 (description and taxonomy of NE. Pacific)

Tapeworms
J 22(3): 865 (candling for *Triaenophorus crassus* cysts in whitefish)
(6): 1335 (*Triaenophorus* procercoids infections of cyclopid copepods)
(6): 1387 (*Triaenophorus*, *Diphyllobothrium*, etc., re Pacific salmons biological information)

Tarr, Hugh Lewis Aubrey
J 22(2): 307 (shrimp nucleotides)
(3): 755 (freeze-dried fish)
CVG 34 (effect of antioxidants on herring meal)
S 889 (fish microbiology)
894 (lingcod muscle enzymes)
897 (salmon milt extract)
969 (antioxidant treatment of herring meal)

Taxonomy (*see also* Speciation; Systematics)
J 22(2): 475 (Plecoptera)
(5): 1151 (two species of NE. Pacific Alepocephalidae)
S 937 (Trematoda genera *Bacciger* and *Pentagramma*)

Teeth
J 22(2): 259 (comparisons in rare Nfld skates)

Teleostomi
J 22(1): 203, 215 (electropherograms re biochemical systematics)

Temperature, water (oceanographic)
J 22(6): 1321 (re marine climate off Canadian Maritimes)
CPO 1965-4 (mean monthly surface, at B.C. coastal stations)
S 956 (Caribbean Sea)

Temperature, water (reactions to)
J 22(2): 503 (selection by DDT-treated young Atlantic salmon)
(3): 825 (re marine ostracod distribution)
(4): 913 (re char eggs mortality and development rate)
(5): 1213 (re pygmy whitefish biology)
(6): 1455 (re goldfish acclimation and ionic regulation)
S 950 (Iles-de-la-Madeleine herring in commercial fishery)

Templeman, Wilfred
J 22(1): 237 (abnormalities in skates)
(2): 259 (rare skates of Newfoundland)
(4): 899 (distinguishing *Raja* species)
(6): 1345 (lymphocystis disease in American plaice)
S 886 (ICNAF research report, 1962)
949 (ICNAF research areas)

Teredo navalis (a mollusc) (*see* Shipworms)

Thaleichthys pacificus (*see* Eulachon)

Thawing
J 22(3): 783 (re thaw-drip of Atlantic cod fillets)

Theragra chalcogrammus (*see* Whiting (Pacific))

Thermal effects (*see* Temperature)

Thomas, Martin Lewis Hall
J 22(3): 695 (migrating sea lamp..ys)
(3): 851 (manganese deposits on molluscs)

Thunnus alalunga (*see* Albacore)

Tibbo, Simeon Noel
S 950 (water temperature and herring fishing)
956 (fisheries research in Caribbean Sea)

Tides
J 22(6): 1425 (re intertidal algae distribution)

Tomlinson, Neil
J 22(3): 653 (chalkiness in halibut)
(3): 775 (post-spawning death of salmon)
(3): 849 (myxosporidian parasite)
(4): 955 (partial freezing of salmon)
S 947 (sodium, potassium, and magnesium in fish)

Tooth (*see* Teeth)

Toxicity (*see also* Shellfish toxicity)
J 22(2): 425 (Cu–Zn solutions to young Atlantic salmon)
(2): 635 (probable, of mummichogs to warm-blooded animals)
S 931 (of Cu and Zn solutions to Atlantic salmon)
963 (mathematical analysis of, re juvenile coho environment)

Transplantation (*see* Species, introduced)

Transport, mass
J 22(1): 159 (theory re fish-egg respiration)

Trawl, otter
S 928 (catch size effect on selectivity for flatfish)

Trematoda (*see* Flukes)

Triaenophorus species (*see* Tapeworms)

Triglycerides (*see* Acids, fatty; Lipids)

Trolling
CPO 1965-6 (Strait of Georgia commercial coho catches)

Trout, alpine (*see* Char, alpine)

Trout, brook (*Salvelinus fontinalis*) (speckled trout)
J 22(2): 335 (swimbladder size re buoyancy of young)
(2): 395 (stream population changes re silt)
(3): 738 (in Kananaskis River system, Alta.)
(3): 767 (and hybrids biochemical differentiation)
S 893, 905, 965 (investigation and management research program, 1962–63, 1963–64, 1961–62)
911 (suitability of barachois ponds for)

Trout, brown (*Salmo trutta*)
J 22(3): 738 (in Kananaskis River system, Alta.)
(3): 767 (and hybrids biochemical differentiation)

Trout, cutthroat (*Salmo clarkii*)
J 22(3): 739 (in Kananaskis River system, Alta.)

Trout, lake (*Salvelinus namaycush*) (*Cristivomer namaycush*)
J 22(3): 744 (in Bow River system, Alta.)
(3): 761 (corneal lesions in hatchery-reared)
(3): 767 (and hybrids biochemical differentiation)
(4): 999 (movements of hatchery-reared in Lake Superior)
(6): 1571 (in fall domestic fishery at Snowdrift, Great Slave Lake)
B 149: 18, 121 (Great Lakes, catches)
S 946 (Great Slave Lake fishery)

Trout, rainbow (*Salmo gairdnerii*)
J 22(3): 713 (oral immunization against "redmouth disease")
(3): 740 (in Kananaskis River system, Alta.)
(3): 767 (and hybrids biochemical differentiation)
(4): 891 (ketone bodies in blood of starved pre-spawning)
(4): 955 (canning after holding partially frozen)
S 893, 905, 965 (investigation and management research program, 1962–63, 1963–64, 1961–62)
911 (suitability of barachois ponds for)
943 (gonadal cell culture stimulation by serum)
947 (Na, K, Mg ion concentration and weight changes re rigor)
962 (effect of salmon pituitary hormones on gonads of immature)

Trout, speckled (*see* Trout, brook)

Trout, steelhead (*Salmo gairdnerii*)
J 22(1): 167 (mass transport theory for egg respiration)
(1): 203 (biochemical systematics)
(4): 1035 (behaviour, ecology, interaction, re young coho)
(5): 1175 (*Piscicola* freshwater leech parasitism)
S 897 (mononucleotide synthesis by milt extract)
925, 926 (INPFC Canadian research reports, 1962, 1963)

Trout, Yellowstone cutthroat (*Salmo clarki lewisi*)
J 22(1): 203 (biochemical systematics)

Trout-perch (*Percopsis omiscomaycus*)
J 22(3): 744 (in Bow River system, Alta.)
(4): 969 (Algonquin Park, Ont., distribution)

Tsuyuki, Hiroshi
J 22(1): 203 (muscle myogens of vertebrates)
(1): 215 (*Oncorhynchus* species identification)
(3): 767 (salmonid hybrids)
S 962 (pituitary hormones of salmon)

Tullibee
B 149: 21, 119 (Great Lakes, catches)

Tully, John Patrick
S 917 (oceanographic region in the north Pacific)

Tunas
S 935 (chilling and freezing on board vessels)
956 (Canadian research in Caribbean Sea)

Turtle, leatherback (*Dermochelys coriacea coriacea*)
S 945 (dermal oil fatty acids)

U

Ungava Bay
J 22(1): 69 (decapod *Argis dentata* larvae and megalopa)

Uthe, John Frederick
J 22(4): 955 (partial freezing of salmon)

V

Vanstone, William Edward
J 22(1): 203 (muscle myogens of vertebrates)
(1): 215 (*Oncorhynchus* species identification)

Vernon, Edwin Herman
S 952 (odd-year pink salmon in the IPSFC convention area)

Vertebrae
J 22(1): 237 (abnormalities in thorny skate)

Vessels, fishing
S 935 (preservation of catch aboard)
946 (Great Slave Lake fleet, 1945–63)

Viscera
J 22(1): 131 (lipids and component fatty acids of squid)

Vitamin B group
S 915 (B_{12} re structure and reactions of cobamide coenzymes)
929 (analysis of cod protein concentrate)

Vladykov, Vadim Dmitrovich
J 22(1): 139 (*Lampetra richardsoni*)

Vosella modilus (*see* Mussel, horse)

W

Waldichuk, Michael
J 22(3): 801 (water exchange and waste disposal)
S 892 (water pollution)
907 (foams in kraft pulp and newsprint effluents)
918 (sea-level oscillations)
941 (radioactive contamination)

Walleye (*Stizostedion vitreum vitreum*) (yellow walleye; yellow pickerel; yellow pike; doré; yellow pikeperch)
B 149: 19, 122 (Great Lakes, catches)

Walleye, blue (*see* Pike, blue)

Walleye, yellow (*see* Walleye)

Watson, Nelson Herbert Frank
J 22(6): 1335 (natural infections of cyclopid copepods)

Watt, Alexander
J 22(3): 793 (phytoplankter enzymes)

Webb, Donald Wayne
J 22(5): 1123 (limnology of Cedar Lake)

Weight (*see also* Length–weight ratio)
J 22(2): 465 (trends in Nfld. longlined cod)
S 947 (changes of fish held in refrigerated sea water re rigor)

Weinstein, Harvey Marvin
J 22(1): 83 (glycolytic activity in cod muscle)

Werner, Arthur Eugene
S 959 (suspended solids from mill effluents)

Westrheim, Sigurd Jergen
J 22(1): 231 (northern range of rockfish)
(6): 1559 (widow rockfish)

White, Harley Clifford
J 22(2): 635 (killifish)

Whitefish, lake (*Coregonus clupeaformis*)
J 22(3): 732 (in Bow River system, Alta.)
(3): 865 (candling fillets for tapeworm cysts)
(5): 1197 (populations year-class fluctuations in Lake Erie, and other large lakes)

(6): 1571 (in fall domestic fishery at Snowdrift, Great Slave Lake)
B 149: 18, 118 (Great Lakes, landings)
S 946 (Great Slave Lake fishery)

Whitefish, mountain (*Prosopium williamsoni*)
J 22(3): 733 (in Kananaskis River system, Alta.)

Whitefish, pygmy (*Prosopium coulteri*)
J 22(5): 1229 (growth and morphometry of four B.C. populations)

Whitefish, round (*Prosopium cylindraceum*) *P. quadrilaterale*) (menominee)
B149: 22 (Great Lakes catch)

Whitetip (*Pterolamiops longimanus*)
S 956 (Canadian research in Caribbean Sea)

Whiting (Pacific) (*Theragra chalcogrammus*)
J 22(1): 203 (biochemical systematics)
(5): 1107 (liver lipid fatty acids)

Wickett, William Percy
CPO 1965-6 (coho commercial troll catches)

Widdowson, Thomas Benjamin
J 22(6): 1425 (distribution of intertidal algae)

Wilder, Donald George
CSG 45 (message to lobster fishermen)

Wiley, William Lloyd
J 22(4): 1025 (recording of fish movements)

Williams, Peter Montague
J 22(5): 1107 (marine fatty acids)

Winnipeg, Lake
S 900 (availability of fishes)
908 (limnology)

Winnipegosis, Lake
S 900 (availability of fishes)

Wittenberger, Carol
J 22(6): 1397 (carp metabolism)

Wood borers
S 948 (dispersal of introduced species in B.C. coastal waters)

X

X-ray
S 934 (angiography of Pacific salmon)

Xiphias gladius (*see* Swordfish)

Y

Yurkowski, Michael
J 22(1): 17, 27 (carbonyl compounds in cod)
(3): 643 (lysolecithinase of cod)

Z

Zinc compounds
J 22(2): 425 (lethal levels Zn–Cu pollutants to salmon)
(4): 929 (re oxidative rancidity promotion in cod flesh)
S 931, 961 (toxicity for Atlantic salmon)
941 (radioactive Zn^{65} seawater contamination)

Zooplankton
J 22(1): 69 (decapod *Argis dentata* in Ungava Bay)
(2): 543 (Canadian Arctic, NW. Canadian Atlantic, Beaufort Sea)
(5): 1107 (lipid fatty acids of marine)
CPO 1965-3, 5, 7, 8 (Strait of Georgia)
S 908 (of Canadian large lakes)

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21. STEWART, JAMES E., AND H. E. POWER. Unit suitable for holding and displaying live lobsters. 6 p.

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